Rhodora

JOURNAL OF THE

NEW ENGLAND BOTANICAL CLUB

Vol. 73 September, 1971 No. 795

BIOSYSTEMATIC STUDIES IN THE NORTH AMERICAN GENUS SABATIA (GENTIANACEAE)[1]

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Sabatia is a herbaceous genus of seventeen species and two varieties which are indigenous to continental North America and the West Indies. They are distributed from central Mexico northward to Nova Scotia and from Oklahoma and Texas eastward to the Atlantic coast.

Although the genus has been subjected to previous revisional treatments (Grisebach, 1839, 1845; Blake, 1915; Wilbur, 1955) and to numerous regional interpretations, very little has been published concerning its cytological and crossing characteristics or breeding systems. Accordingly, this investigation is biosystematically oriented.

HISTORICAL ACCOUNT

The genus *Sabatia* was proposed by Adanson (1763) to commemorate an Italian botanist, Liberato Sabbati. Plants belonging to the genus had been described earler by Gronovius (1739) as species of *Gentiana*. Linnaeus (1753) treated the four species known to him as representatives of the

[1]Based on a dissertation presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Botany at Duke University. Voucher specimens of species and hybrids are deposited in the herbarium of Duke University.

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genera *Chironia* and *Swertia*. Later he transferred one of the species from *Chironia* to *Chlora*.

Pursh (1814) accepted *Sabatia* and extended it to include the American species placed in *Chironia*. The genus was treated in Grisebach's (1839, 1845) monographs of the Gentianaceae in which were recognized 11 species and one variety. Gray (1878) included 13 species and two varieties in his "Synoptical Flora." Blake (1915) recognized 22 species and one variety which were grouped into subgenera, sections, and subsections. Wilbur (1955) recognized 17 species and two varieties in a systematic hierarchy basically similar to that of Blake.

SYNOPSIS OF TAXA

The following synopsis of *Sabatia* is based upon Wilbur's (1955) treatment which provides the framework for these investigations. Emended descriptions and notes on the ecology, phenology, and distribution of each species are presented. Nomenclatural history, keys, full descriptions, and range maps are given by Wilbur and are not repeated here.

Section I. SABATIA.

Annuals, biennials, or perennials. Branches opposite or alternate. Flowers pedicellate, solitary, or loosely cymose; pentapetalous (annuals and biennials only) or pluripetalous; pink or white. Bracts subtending flowers small and scale-like. Anthers becoming revolutely coiled after pollen release, or recurved. Stigmatic branches usually coiled at maturity. Five subsections, 15 species.

This section contains the type species *S. dodecandra* and must bear the generic name unaltered according to Art. 22, International Code of Botanical Nomenclature (Lanjouw, 1961).

Subsection A. DIFFORMES Wilbur, Rhodora 57: 6. 1955.

Perennials, with thick elongated rhizomes. Branches typically opposite. Flowers pentapetalous (the first and innermost larger, occasionally 6-parted), white. Anthers becoming recurved after pollen release. Stigmatic branches

coiled at maturity. Basal rosette formed during dormancy. Two species.

Sabatia difformis (L.) Druce, Bot. Exch. Club and Soc. Brit. Is. **3**: 423. 1914.

Calyx lobes usually more than 4 mm long. Corolla lobes longer than 7 mm. Leaves and upper portion of stem not glaucous. Main stem and branches usually strongly angled.

Sabatia difformis occurs in savannas and pine barrens from central New Jersey southward through peninsular Florida and into western Florida. Individuals have been collected for this study from a river bank in western Florida and from roadside ditches in North Carolina. The species has a weedy habit and may rapidly invade newly cleared areas.

Stems die in the fall, and during winter dormancy one or more small basal rosettes grow from the rhizome. The lowermost leaves are subterranean. With elongation in spring these become cauline leaves. Flowering occurs from late May through late August. Under greenhouse conditions the time from pollination to seed release from the capsule is about three months. Approximately 165 seeds per capsule are produced by artificial selfing. This and subsequent estimates of seed set are based on a minimum of ten self-pollinations.

Sabatia macrophylla Hook., Compan. Bot. Mag. **1**: 171. 1836.

Calyx lobes less than 4 mm long. Corolla lobes to 7 mm in length. Leaves and upper portion of stem glaucous. Main stem and branches terete throughout.

Two varieties have been recognized. *Sabatia macrophylla* var. *macrophylla*, having short erect calyx lobes less than or equalling the tube in length, ranges from northwestern Florida and Georgia into Louisiana. *Sabatia macrophylla* var. *recurvans* (Small) Wilbur grows in northeastern Florida and southern Georgia. It has recurved calyx lobes exceeding the tube in length. Both varieties occur in savannas and pine barrens; var. *macrophylla* grows in open flatwoods, swampy meadows, bogs, and on moist grassy slopes. *Sabatia macrophylla* var. *recurvans* grows in seepage areas

which are often wooded, in elevated slash flatwoods and moist sandy savannas, and occasionally in open bogs.

The varieties occupy distinctive geographical ranges which converge in the vicinity of Lake City, Florida. In calyx-lobe length and recurvation, individuals at the western limit of var. *recurvans* do not resemble var. *macrophylla*. In the eastern portion of its range, however, var. *macrophylla* occasionally has a slight recurving of the calyx lobes; the lobes may be longer, though not exceeding the calyx tube in length. Whether this variation in calyx lobe recurvation is sporadic or continuous from west to east has not been determined. No population containing both varieties was located.

Winter dormancy is similar to that of *S. difformis*. The lowermost leaves of the rosette are subterranean. Standing water often covers the plants before elongation in early spring. Flowering occurs from mid-June through July. Under greenhouse conditions the time from pollination to seed release from the dried capsule is about three months. Approximately 90 seeds are produced by artificial selfing.

Subsection B. ANGULARES Blake, Rhodora **17**: 56. 1915.

Biennials, with fibrous roots. Branches typically opposite. Flowers pentapetalous, corollas pink or white. Anthers becoming circinnately recoiled after pollen release. Stigmatic branches tightly coiled at maturity. Basal rosette well-developed and often persisting through anthesis. Three species.

Sabatia angularis (L.) Pursh, Fl. Am. Sept. **1**: 137. 1814.

Corollas pink (rarely white). Calyx lobes usually 1.5 mm or more wide. Lower cauline leaves usually broadly ovate or ovate-lanceolate, often strongly clasping. Lower portion of stem strongly 4-angled, the corners membranous.

Sabatia angularis is the most widespread representative of the genus, ranging from southern New York to northern Florida and westward to Ohio, Illinois, and Texas. Populations occur in fields, prairies, and along margins of woodlands, often near roadsides. Habitats vary from alluvial plains through low, poorly drained pine woods, weedy, clay

roadside banks, and steep slopes of ravines to rich pine-hardwood forests. Large populations grow on granite outcrops in Georgia.

Wilbur (1955) noted that some confusion exists as to whether the species of subsection *Angulares* are annual or biennial; he concluded that they are probably all annuals. Field and greenhouse observations indicate that the species are biennial. Where flowering specimens of *S. angularis* have been seen in the field, nearby rosettes were identical to the persistent rosettes of flowering individuals. Efforts to transplant non-flowering plants to a greenhouse were unsuccessful.

Germination results in a rosette which persists during the first summer and winter; flowering occurs during the second summer. The time of germination in the field was not determined, but it is probably not until spring. The possibility of winter dormancy was investigated. Seeds from selfed pollinations were collected from one plant (*Perry* 1303c, Durham Co., N.C.) and separated into two treatments: half were stored for six months at 35°F; the remainder were stored at room temperature (74°F) for the same amount of time. At the end of this period seeds were sown on filter paper in petri dishes. Those seeds subjected to the cold treatment germinated within nine days and within 20 days all except 12 of the 300 seeds had germinated. Seeds not preconditioned germinated slowly. Two of 300 seeds germinated in 20 days, and germination subsequently was sporadic. Overall germination at the end of 40 days was 96% for preconditioned seeds and 44% for untreated seeds.

Two additional tests were made. First, seeds were sown on filter paper immediately after collection from a mature capsule (*Perry* 1890a, Oglethorpe Co., Ga.). Of 450 seeds, 67% germinated in 40 days. Second, seeds (*Perry* 1303a) which had been stored for two years at 74°F were sown; 58% germinated of 300 seeds. These germination tests show that a period of preconditioning at low temperatures enhances the rate and percentage of germination, but afterripening is not necessary for germination. Seedlings grown

in the greenhouse, however, will not elongate unless subjected to low temperatures for three or more months.

Flowering is in July and August. Once an individual has flowered, the plant invariably dies, i.e., it is monocarpic. Efforts to produce additional growth from the roots failed. Under greenhouse conditions mature seeds are released three months after pollination. About 500 seeds per capsule are produced by artificial pollination.

Sabatia quadrangula Wilbur, Rhodora **57**: 22. 1955.

Corolla white. Calyx lobes less than 0.5 mm wide. Lower cauline leaves usually oblong, infrequently ovate, often strongly clasping. Lower portion of stem strongly 4-angled, the corners membranous.

Sabatia quadrangula is distributed from southeastern Virginia to central Florida. It is found more frequently in the Piedmont of North and South Carolina than in the Coastal Plain. Plants grow in fields and pinelands, along borders of pocosins, in sandhills, in savannas and flatwoods and in shallow islands of soil on granite outcrops.

Sabatia quadrangula is biennial. A large population occurs on the Anglin Farm granite outcrop in Walton Co., Georgia. Collections were made there in July, 1965, and again in 1966. On both occasions numerous rosettes, identical with the persistent rosettes of flowering specimens, were found. Efforts to transplant these were unsuccessful. The developmental sequence as outlined for *S. angularis* is apparently the same in *S. quadrangula*. Plants are monocarpic. Flowering occurs from mid-June through early July. Fully developed seeds are released about three months after pollination under greenhouse conditions. About 400 seeds per capsule are ordinarily produced by artificial pollination.

Sabatia brachiata Ell., Sk. Bot. S.C. & Ga. **1**: 284. 1817.

Corolla pink (rarely white). Calyx lobes less than 1 mm wide. Lower cauline leaves oblong or elliptic, not strongly clasping. Lower portion of stem terete.

Sabatia brachiata grows from eastern Virginia into Georgia and westward to southern Missouri and Louisiana.

Typical habitats are fields, roadsides, savannas, oak woods, and dry, open pine woods. It is capable of growing in very dry, sandy areas or in low, poorly drained pine woods, ditches, and boggy meadows.

The species is biennial and has basically the same maturation pattern as outlined for other members of the subsection. In summer of 1966, rosettes of *S. brachiata* from Pender Co., N.C., were transferred successfully to the greenhouse. One plant under increased photoperiod and a warm temperature regime elongated during the winter and flowered. Rosettes kept under a cool winter regime were much larger and more robust the following spring.

Sabatia brachiata is not strictly monocarpic. In the greenhouse, plants often survived to flower a second time the following year. Flowering is in June and July. Under greenhouse conditions development of seeds from pollination takes about 4 months. About 450 seeds per capsule are produced by artificial pollination.

Subsection C. CAMPESTRES Blake, Rhodora **17**: 56. 1915.

Annuals, with fibrous roots or a well-developed taproot. Branches alternate. Corolla pentapetalous, pink (rarely white). Anthers recoiled or not at pollen release. Stigmatic branches coiled or not at maturity. Calyx tube very prominently 5-nerved. Basal rosette none. Two species. This subsection is treated as a section (see "Taxonomic Relationships").

Sabatia campestris Nutt., Trans. Am. Phil. Soc. n.s. **5**: 197. 1835.

Leaves and calyx lobes thin and membranous. Calyx lobes 2-6 times longer than the calyx tube and exceeded by the corolla lobes. Anthers 3-6 mm long, becoming circinnately recoiled after pollen release. Stigmatic branches over 5 mm long, becoming strongly coiled at maturity.

Sabatia campestris ranges from Illinois and Missouri south through Oklahoma and eastern Texas, and occasionally eastward to Mississippi. Plants occur in fields and prairies and often along roadsides. The soil is usually dry and sandy, although wet grassy bottoms and alluvial plains

furnish good growing conditions as well. Individuals sometimes grow in open woods. Plants under unfavorable growth conditions rarely branch, are much reduced in height, and produce from one to six flowers. When grown in a greenhouse under favorable conditions, there is considerable branching, increased height growth, and production of 18-50 or more flowers.

Flowering is from mid-June through July in most of the range. Plants are strictly monocarpic. Seeds are produced in about four months under greenhouse conditions. The maturing capsules remain green for a considerable time after the plant dies; they eventually turn brown and dehisce while still within the confines of the dried calyx tube. About 750 seeds per capsule are produced by artificial pollination.

Sabatia arenicola Greenm., Proc. Am. Acad. 34: 569. 1899.

Leaves and calyx lobes thick and succulent. Calyx lobes less than twice the calyx tube length and exceeding the corolla lobes. Anthers about 2 mm long, straight or slightly recoiling after pollen discharge. Stigmatic branches 2-4 mm long, becoming merely flattened and recurved at maturity.

Sabatia arenicola is restricted to beaches and dunes from Louisiana westward to Texas and southward into Mexico. The species often grows just behind the fore dunes and on both sides of succeeding dunes. Such individuals are low and form many short, spreading branches and a long taproot. There is a pronounced succulence of leaves and calyx lobes. Under greenhouse conditions, branching is much less profuse and root growth tends to be fibrous. The succulence of leaves and calyx lobes is maintained.

Flowering occurs from mid-June through early July, and the plants are strictly monocarpic. Seeds are produced in about 2 1/2 months in the greenhouse. Both in the field and greenhouse, *S. arenicola* plants die shortly after flowering. The capsules remain green for a longer period, although growth in size ceases. During this time the capsules remain fleshy and the seeds are soft and saturated with

moisture. Eventually the capsule darkens and dries, and the seeds lose their moisture and assume the characteristic dark color. The capsule dehisces while enclosed within the dried calyx tube. About 500 seeds per capsule are produced by artificial pollination.

Subsection D. CAMPANULATAE Blake, Rhodora **17**: 56. 1915.

Annuals or perennials with fibrous roots, a thin taproot, or a perennating caudex. Branches alternate. Flowers pentapetalous; corolla pink or white. Anthers circinnately recoiled after pollen release. Stigmatic branches coiled at maturity. Basal rosette present or not. Four species.

Sabatia campanulata (L.) Torr., Fl. N. & Mid. U.S. 217. 1824.

Perennial, growing from a short branching underground caudex; often with 2 or more aerial stems. Corolla pink (rarely white). Calyx lobes usually more or less equalling the corolla in length. Leaves oblong, narrowly oval, or linear, usually widest below the middle. Rosette formed by new growth during winter, not persisting.

Sabatia campanulata grows in the Coastal Plain from Massachusetts to northern Florida and westward to Louisiana and Arkansas; and locally inland in Tennessee, Indiana, Illinois, Kentucky, and Arkansas. The species grows in bogs and savannas, often in low, poorly drained meadows and marshes, and occasionally along roadsides.

Within the species there is considerable variation in leaf shape, calyx- and corolla-segment lengths, and degree of branch divergence. This led to recognition of a separate species, *S. gracilis* (Fernald, 1932), having linear leaves, smaller flowers, more divergent branches, and a Coastal Plain distribution from Florida to Louisiana and southeastern Virginia. Later, specimens were found with features of both species and Fernald (1937) concluded they should be treated as geographic varieties. Wilbur (1955) was unable to find consistent differences between the two populations and relegated *S. gracilis* to synonymy with *S. campanulata*.

Wilbur's conclusion is supported by my field and greenhouse observations. Leaf shape, calyx and corolla lengths, and branching are strongly influenced by the habitat. Mass collections from populations in Florida revealed that plants growing among dense clumps of grasses in a savanna or meadow assume the appearance of *gracilis*. The leaves are small and linear, the calyx and corolla segments are narrow and short (less than 15 mm long), and the branches are strongly divergent. Such plants are supported by the surrounding grasses and other vegetation and are so lanky as to be incapable of self-support when the vegetation is removed. By contrast, specimens along roadsides and cleared areas in Florida are self-supporting and often branch considerably from the base. The leaves are larger than in savanna plants and are lanceolate to almost ovate in outline. The calyx and corolla segments may be larger (to more than 2 cm). Branching is strongly ascendant and rigid. Greenhouse progeny of the *gracilis* type take on the typical growth form of *S. campanulata*. Thus, there seem to be no genetically-determined morphologically recognizable subpopulations within the species.

Flowering occurs from mid-June through early August. Development and release of mature seeds takes three months or more from pollination. About 700 seeds per capsule result from artificial pollination.

Sabatia stellaris Pursh, Fl. Am. Sept. **1**: 137. 1814.

Annual, with fibrous roots; usually with one main stem having branches borne on the upper half of the stem. Corolla pink (rarely white). Calyx lobes extending 3/4 the length of the corolla. Leaves linear to obovate, usually widest above the middle. Rosette not formed.

Sabatia stellaris grows along the coast from southern Massachusetts to Louisiana and extends inland in Florida and Mexico. The species is confined to salt marshes, adjacent littoral areas, and swales except in Florida, Mexico, and certain Bahama islands.

Wilbur (1955) noted variation similar to that described for *S. campanulata*. Florida specimens tend to be elongate,

wiry, and slender with narrowly linear leaves. Northern individuals are more compact, less branched, and have broadly elliptical leaves. Wilbur concluded that the differences are not sufficiently constant for recognition of subspecific categories. Collections made for the present study support this conclusion. Individuals growing in a partially cleared area in southern Florida were stocky, robust plants resembling northern material in leaf shape and branching. Regardless of their initial site, greenhouse-grown plants when not crowded are sturdy and non-wiry and have nonlinear leaves. A number of field collections and observations have provided convincing evidence that relative wiriness and size of leaves are controlled by competition and associated effects. Much of this variation is lost when transplants or seedlings are grown in a uniform environment.

Britton (1905) and Britton and Millspaugh (1920) recognized two species from the Bahamas, the pink-flowered *S. campanulata* and a white-flowered endemic, *S. simulata* Britton. Wilbur (1955) concluded that all Bahamian material is annual and referable to *S. stellaris*. My collections from four islands in the Bahamas failed to reveal any plants which could be referred to the perennial *S. campanulata*. Plants of *S. stellaris* with pink flowers were found on Eleuthera, Grand Bahama, and Great Abaco islands. These occupied inland sandy areas similar to habitats known for the species in Florida. On New Providence white-flowered forms were found almost exclusively, and these were around salt marshes. Contrary to Britton and Millspaugh (1920), occasional specimens with pink-tinged corollas do occur there also.

Since both pink and white forms sometimes grow sympatrically on Great Abaco, extensive population samples were taken. South of Marsh Harbour, in the "whitelands" of Abaco, exclusively white-flowered individuals were found growing in crevices of the very dry aeolian limestone. These were more succulent in appearance than were any others, and they branched profusely from the base. An individual transferred to the greenhouse developed eight erect flowering stems and numerous shorter lateral branches, while

growing to a height of 29 inches. These "whiteland" individuals probably are differentiated ecotypically from their congeners elsewhere on Abaco and on New Providence.

In moist, low roadside ditches northwest of Marsh Harbour toward Green Turtle Cay, numerous individuals were found with flowers ranging from rose through pink and shades of pink to white. In addition to color, the pattern of the floral "eye" varied. Usually in *S. stellaris* the yellow color at the base of each petal is bordered by an irregular line of maroon or brown color. The border occasionally is lacking. Combinations of these characters were found in the roadside population. A sample of 108 plants was taken and sorted according to floral variation. Forty-seven individuals were found which were florally intermediate between pure white and pink forms. Twenty-seven of these had a strip of white parallel to the border of the "eye." This variation was probably the result of crossing and backcrossing among ancestral populations and suggests that there is no basis for distinguishing *S. simulata*. To study this problem further, white-flowered Bahamian forms were incorporated into the cytological and hybridization programs.

In southern Florida, plants flower throughout the year; elsewhere the flowering time is July and August. Bahamian plants are at a flowering peak in April and May. Seed development takes about two months. An average of 600 seeds per capsule are produced from artificial pollination.

Sabatia grandiflora (A. Gray) Small, Fl. SE. U.S. 928. 1903.

Annual with fibrous roots. Usually one rigid stem with branches confined to the upper third or half of the stem. Corolla pink (rarely white). Calyx lobes mostly less than 3/4 as long as corolla, rarely exceeding it. Leaves rigid, fleshy, those above usually not exceeding the stem in diameter. Lowermost leaves sometimes clustered.

Sabatia grandiflora grows in peninsular Florida and western Cuba. In Florida it grows in the Everglades, in pinelands, along moist sandy roadsides, and along sandy shores of lakes and ponds.

In the greenhouse the lower leaves are not clustered unless the plant has been subjected during early growth to a period of lower temperatures. Individuals growing in standing water in the field frequently have clustered lower leaves.

Flowering occurs primarily in June and July, but occasional flowering specimens have been collected from January through November. Development and release of mature seeds takes two to three months from pollination. Artificial pollination results in about 1100 seeds per capsule.

Sabatia brevifolia Raf., Atlant. Jour. **1**: 147. 1832.

Annual, with a slender branching taproot. One main stem, in robust specimens branching nearly to the base; branches usually alternate and widely divergent, giving a wiry appearance. Corolla white. Calyx lobes about 1/2 as long as corolla, or less. Leaves thin, membranous, above often less than 1 mm wide, below variously shaped and to 7 mm wide. Lowermost leaves broader, forming a rosette and often persisting.

Sabatia brevifolia is distributed from southeastern South Carolina throughout Florida and westward to Alabama. It grows in savannas, pinelands, occasionally in moist to wet sandy peat of bogs, and in the dry white sand border of Florida "scrub islands."

This is the only species known to flower exclusively in late summer and early fall. Flowers are produced from mid-August through mid-October in the northern part of its range and through mid-November in southern Florida. The capsules are mature about three months after pollination. About 200 seeds per capsule are produced by artificial pollination. It is not certain whether germination occurs in the fall or spring. Young seedlings form a rosette which often persists to maturity; the plants are strictly monocarpic.

Subsection E. DODECANDRAE Wilbur, Rhodora **57**: 78. 1955.

Perennials, with rhizomes. Branches usually alternate. Flowers pluripetalous (in *S. calycina* 5- to 7-merous), pink

(rarely white). Anthers recurved or circinnately recoiled after pollen release. Stigmatic branches recurved or coiled at maturity. Basal rosette present or not. Four species.

Sabatia calycina (Lam.) A. Heller, Bull. Torr. Bot. Club **21:** 24. 1894.

Usually 5-6 corolla lobes (rarely 7). Calyx lobes about as many, foliaceous. Leaves broad, spatulate, tapering to an almost petiolate base, considerably broader than the stem. Rosette none.

Sabatia calycina grows along the Coastal Plain from southeastern Virginia. throughout most of Florida, westward to eastern Texas, and in eastern Cuba and central Hispaniola. The species is abundant in the marginal zones of freshwater marshes; it occurs also in moist to swampy lowland hardwood stands, in swamps, in ditches, and often on creek or river banks.

Sabatia calycina was placed by Blake (1915) in his subsection *Campanulatae*, composed of species having flowers with 5 (rarely 6 or 7) petals. My hybridization evidence supports this placement (see "Taxonomic Relationships"). Wilbur (1955) put the species in subsection *Dodecandrae*. There is considerable morphological evidence in support of this. *Sabatia calycina*, in common with the *dodecandra* alliance, has foliose calyx lobes, broad leaves, and a rather leafy seedling. Individuals not excessively branched are much like *S. dodecandra* var. *foliosa*. However, the flowers are smaller and often pentapetalous.

The behavior of stigmatic branches and of anthers at maturity differs from that of other members of the *Dodecandrae* and from the *Campanulatae* as well. The anthers of *S. calycina* become only slightly recurved after pollen release, and the stigmatic branches spread parallel to the upper surface of the flower at maturity. Other species in the *Dodecandrae* possess anthers which become strongly circinnately recoiled after pollen release, and the stigmatic branches become coiled into three or more loops.

Sabatia calycina flowers from early June through July throughout most of its range. Under greenhouse conditions

mature seeds are released three to four months after pollination. Approximately 1000 seeds per capsule are produced by artificial pollination.

Sabatia dodecandra (L.) BSP., Prel. Cat. N.Y. 36. 1888.

Usually 9-12 corolla lobes. Calyx lobes about as many, from inconspicuous to large and foliaceous. Cauline leaves mostly elliptic to oblong, broader than the stem. Rosette formed during winter dormancy, its leaves similar to the cauline leaves.

Two varieties of the species were recognized by Wilbur (1955). *Sabatia dodecandra* var. *dodecandra* grows in brackish marshes from Connecticut into South Carolina and locally in Florida. Each internode exceeds the leaf by 1.5 to 3 times. Stolons are rarely present. Flowering occurs from late June through mid-August, rarely as late as November. In the greenhouse mature seeds are released two to three months from pollination. About 500 seeds per capsule are produced by artificial pollination.

Sabatia dodecandra var. *foliosa* (Fern.) Wilbur grows on river banks and along ponds and streams inland from South Carolina into northern Florida and westward to Louisiana. It may be found in swamps, wet grassy ditches, and low pinelands. The internode is equalled or exceeded by the leaf. Stolons are usually present. Flowering is from mid-June through August. Development and release of mature seeds takes three to four months from pollination. About 2400 seeds per capsule are produced by artificial pollination.

Two other species have been recognized in the *S. dodecandra* complex. Small (1903) proposed *S. harperi.* Blake (1915) concluded that *S. foliosa* (= *S. dodecandra* var. *foliosa* (Fern.) Wilbur) and *S. harperi* Small were conspecific. At the same time Blake (l.c.) described *S. obtusata.* Wilbur (1955) relegated *S. obtusata* Blake to synonymy as a minor variant of *S. dodecandra* var. *foliosa.* The present study has provided no evidence to support recognition of *S. harperi* and *S. obtusata.*

Sabatia kennedyana Fern., Rhodora 18: 150. 1916.

Usually 9-12 corolla lobes. Calyx lobes about as many,

linear and flat, hyaline-margined. Cauline leaves linear to oblanceolate, long-tapering to the base, broader than the stem. Primary branches mostly opposite. Rosette formed during winter dormancy, its leaves similar to the cauline leaves.

Sabatia kennedyana grows from Nova Scotia to South Carolina. In Canada it is found in fresh-water marshes. In the United States *S. kennedyana* grows in eastern Massachusetts, Rhode Island, southeastern North Carolina, and northeastern South Carolina. The species is limited to very wet areas on the Coastal Plain; it is usually found along the margins of ponds and streams or in wet cypress bottomland adjacent to a river or stream. Early growth often takes place under standing water, and the lower half or more of the stem may be submerged. Stolons are usually present.

The species flowers from mid-June through July in North and South Carolina. In Massachusetts, Rhode Island, and Nova Scotia, plants flower from mid-July through August and sometimes later. Development and release of mature seeds take about three months from pollination. About 1300 seeds per capsule are produced by artificial pollination.

Sabatia bartramii Wilbur, Rhodora **57**: 91. 1955.

Usually 10-12 corolla lobes. Calyx lobes about as many, usually succulent and rounded in cross-section, strongly subulate. Cauline leaves narrowly linear, less than to slightly broader than the diameter of the stem, thickened. Rosette leaves broadly spatulate, thickened.

Sabatia bartramii grows in southern Georgia and Alabama, throughout Florida, and to southeastern Mississippi. Typical habitats include savannas, low pine barrens, moist roadside ditches, and cypress lowlands. Plants often grow in standing water.

Flowering occurs from mid-June (sometimes earlier in southern Florida) through mid-August. Development and release of mature seeds take three months from pollination.

Approximately 1300 seeds per capsule are produced by artificial pollination.

Section II. PSEUDOCHIRONIA Griseb., Gen. et Sp. Gent. 125. 1839.

Perennials. Branches opposite or alternate. Flowers nearly sessile, if more than one, capitate; 7-12 parted; pink. Bracts subtending flowers large and leaf-like. Anthers never becoming revolutely coiled or strongly recurved after pollen release, instead remaining erect and rigid, sometimes slightly twisted laterally. Stigmatic branches somewhat recurved at maturity. Two species.

The two species placed in this section, *S. capitata* and *S. gentianoides*, are strongly differentiated from other members of the genus and are easily distinguished from each other. Neither species is an annual as reported (Wilbur, 1955). Some individuals of both species were found to have the previous year's dead stem and fruits still attached. Small rosettes of *S. gentianoides* were often present with flowering specimens in the field. Several of these, transferred to a greenhouse, flowered the following year.

Sabatia capitata (Raf.) Blake, Rhodora **17:** 54. 1915.

Basal and cauline leaves not strongly dimorphic, the cauline elliptic or oblong, usually obtuse; the basal similar or broader and shorter. Calyx lobes linear, often unequal, erect.

Sabatia capitata has the most restricted range of any species in the genus. It is known now in northwestern Georgia, although in the 19th century its range extended into southeastern Tennessee, northeastern and central Alabama, and perhaps to southwestern North Carolina. Prior to this study, only three collections of the species had been made after 1900, one from Alabama, the others from Georgia.

Sabatia capitata grows in open hardwoods on moderately dry hillsides and ridges, or occasionally in moist lowland woods. Plants used in this study were collected along the crest of Pigeon Mountain in Walker Co., Georgia. There they grew scattered in open patches of ground in an oak-

hickory stand. Doctor Philip F.-C. Greear of Shorter College has located a disjunct population growing in silicious chert in Bartow Co., Georgia; a limited number of plants were removed for study.

Flowering occurs from late June through mid-August. A period of 2 1/2 to three months from pollination is required for development of mature seeds. About 750 seeds per capsule are produced by artificial pollination.

Sabatia gentianoides Ell., Sk. Bot. S.C. & Ga. **1:** 286. 1817.

Basal and cauline leaves strongly dimorphic, the cauline narrowly linear, width equal to or less than the diameter of the stem; the basal broad, oblong to orbicular spatulate. Calyx lobes subulate, the tips usually reflexed.

Sabatia gentianoides ranges from North Carolina into Florida and westward into eastern Texas on the Coastal Plain. It grows chiefly in savannas and pinelands, occasionally in open bogs, boggy meadows, roadside ditches, and on dry roadside banks.

In North Carolina the species has peak flowering in August, beginning sometimes in mid-July and extending occasionally to mid-October. To the south, flowering is at its peak in July. Development of mature seeds in a greenhouse takes two to three months from pollination. About 1200 seeds per capsule are produced by artificial pollination.

BREEDING SYSTEMS

All species of *Sabatia* are self-compatible. Apomixis is ruled out since emasculated flowers fail to set seed and artificial hybrids combine traits of both parents. While all species are capable of autogamous reproduction, the majority are protandrous. The difference in time between stigmatic receptivity and anther dehiscence varies with the species, and dichogamy may be partial to complete. Outcrossing is favored also by physical separation of the stigma and anthers. In most species the filaments, which were erect at pollen release, bend toward the corolla and away from the expanding stigmatic branches. It thus becomes unlikely that any remaining pollen could be transferred by mechanical means to the stigma.

In *S. difformis* and *S. macrophylla* the outermost flowers in the cymules mature last and are frequently staminate. A small ovary and style may be present, but the stigmatic lobes never extend above the corolla tube. Staminate flowers have not been observed in the other species. A loss of vigor which accompanies end-of-season flowering accounts for the staminate expression; its effect on outcrossing is probably negligible.

The breeding system was studied in the field and greenhouse. Table 1 summarizes floral maturation data obtained from plants growing under uniform conditions in a greenhouse. Observations were made concurrently on all species, except *S. brachiata*, during a time of consistently warm, clear weather. The overall developmental sequence is slowed somewhat by cloudy or cool weather, or both, but successive events seem to be relatively constant.

Full release of pollen from mature anthers takes less than 24 hours, but some pollen may adhere for longer periods. After dehiscence the anthers become dry and often drop from the filaments. In seven species this occurs one or two days before the stigmatic branches are receptive. Eight species show partial overlap in stigmatic receptivity and presence of pollen. However, the stigmata are never receptive, or even uncoiled, on the same day that pollen is fully released. In the field, where wind and insects will shake the flowers and remove pollen, it is less likely that pollen will be left at the time stigmatic branches are receptive.

The comparatively unrelated *S. calycina* and *S. arenicola* are not protandrous. Stigmatic surfaces are receptive on the same day pollen is fully released. Floral structures are such that the stigmatic branches are invariably brought into contact with the dehiscing anthers and autogamy is assured. Seed set by both species is high. Prevention of pollen transfer by wind or by insects does not affect seed set.

Moore and Lewis (1965) have shown that the evolution of self-pollination frequently is associated with morpholog-

TABLE 1

Sequence of events in anthesis of *Sabatia* flowers. Values are given in consecutive days. The first day in each case is that on which expansion of the flower bud began.

Taxa	Developmental Sequence							
	Bud Opening	Petals Extended	Anthers Recurving	Anthers Dehiscent	Pollen Shed	Stigma Uncoiling	Stigma Receptive	Maturation Overlap
Section *Sabatia*								
Subsect. *Difformes*								
S. difformis	1	2	2	3	5	6	7	none
S. m. var. *macrophylla*	1	2	2	2 - 3	4	5	6	none
S. m. var. *recurvans*	1	2	2	3	4	5	6	none
Subsect. *Angulares*								
S. angularis	1	2	1	2	7	4	5	partial
S. brachiata	1	2	2	3 - 4	8	6	7	partial

Subsect. *Campestres*								
S. campestris	1	2	2	3	7 - 8	7	8	partial
S. arenicola	1	2	2	3	6	2	3	complete
Subsect. *Campanulatae*								
S. campanulata	1	2	2	3	4 - 5	5	6	none
S. stellaris	1	2	2	3	4	4	5	none
S. grandiflora	1	2	2	3	7	5	6	partial
Subsect. *Dodecandrae*								
S. calycina	1	2	2	3	7	2	3	complete
S. d. var. *dodecandra*	1	2	2	3	5	5	6	none
S. d. var. *foliosa*	1	2	2	3	6	4	5	partial
S. kennedyana	1	2	2	3	5 - 6	4	6	partial
S. bartramii	1	2	2	3	7	5	6	partial
Section *Pseudochironia*								
S. capitata	1	2 - 3	–	4	8 - 9	5	6	partial
S. gentianoides	1	2	–	2 - 4	5	5	7	none

ical and cytogenetic differentiation. There is relaxed selection for conspicuous flowers and positive selection for smaller flower parts, excluding the ovary. However, the essential change is either early maturation of the stigma (Moore and Lewis, l.c.) or retarded anther dehiscence (Breese, 1959). A reduction in chromosome number is generally correlated with simplification of the life cycle, reduction in size, and increase in uniformity of the breeding system (Grant, 1956a).

Additionally, an autogamous breeding system is most likely to arise in annuals or short-lived perennials which inhabit temporary or marginal areas (Stebbins, 1957; Moore and Lewis, 1965). Abundant seed production from year to year is assured, and ". . . the descendants of a single well-adapted initial colonizer will be equally well-adapted to these same conditions . . ." (Stebbins, 1957). Self-pollination is also advantageous when environmental conditions reduce pollinator activity (*cf.* Haskell, 1953; Ornduff, 1966).

These correlated responses are associated with the autogamous breeding system in *Sabatia*. *Sabatia arenicola* is a small monocarpic annual which is restricted to beaches and dunes. The flowers are reduced in size; the ovary, however, is large. Stigmatic branches are receptive when the anthers dehisce, and mechanical transfer of pollen is assured by the proximity of anthers and stigmas. The chromosome number (n=14) is one of the lowest in the genus, and the developmental cycle one of the shortest.

Sabatia calycina is a polycarpic short-lived perennial. The plant is somewhat reduced in size, and flowers are smaller than are those of other members of subsection *Dodecandrae*. It is capable of flowering the first year. Stigmatic branches are receptive when the anthers dehisce, and there is mechanical transfer of pollen. The paludal habitats of this species may be stable or, if by moving water, unstable. It has a polyploid chromosome number (n=32).

Evolution of the inbreeding system in *Sabatia* appears to have been favored by positive selection for early maturation of the stigma. Associated morphological parallelisms,

such as reduction in flower size, have evolved, though outcrossing is not structurally prohibited. Thus, there is a degree of breeding duality which can meet the conflicting demands of immediate fitness and long-term flexibility and which is adaptively beneficial under varying environmental stresses.

POLLINATORS

Published reports and my field observations show that the larger-flowered outcrossing Sabatias are pollinated primarily by bumblebees *(Bombus)* and that the smaller-flowered species, incapable of supporting the weight of a bumblebee, are visited by lighter bees (often of family Halictidae). Species of *Bombus* (family Apidae) were collected from flowers of *S. bartramii* (*Bombus impatiens* Cresson) and of *S. capitata* (*B. pennsylvanicus* [DeGeer]). Pollen grains of *Sabatia* were found in the corbiculae of each bee. There appears to be a certain amount of flower inconstancy, since pollen grains of other species were found with those of *Sabatia*.

Augochloropsis metallica metallica (Fabricius), family Halictidae, was collected from *S. kennedyana* and *S. macrophylla* var. *recurvans*. Collections of *Halictus* sp. (Halictidae) were made from *S. campanulata*, and pollen from the insects' bodies resembled that of *S. campanulata*.

Coleopteran visitors included *Phyllophaga rugosa* (Melsheimer), family Scarabaeidae; cf. *Anisosticta*, family Coccinellidae; and *Epicauta* cf. *lemniscata* (Fabricius), Meloidae. *Sabatia* pollen grains in most instances were found on the mouthparts. The flower spiders *Xysticus* sp. and *Misumenoides aleatorius* (Hentz) are commonly associated with *S. macrophylla* but do not aid in cross-pollination.

Mitchell (1960, 1962) listed three additional species of *Sabatia* pollinators. With revised nomenclature the flower records were attributed to Robertson (1929) whose collections were made from *S. angularis*. Robertson identified *Ceratina (Zadontomerus) dupla dupla* Say, Xylocopidae; cf. *Augochlorella aurata* (Smith), Halictidae, as *Oxysto-*

glossa similis; and *Megachile (Litomegachile) brevis brevis* Say, Megachilidae.

A detailed description of floral adaptation for pollinators is given by Hill (1891) for *S. angularis*. He reported that the anther walls are stretched as the anther recurves, and that pollen is forcibly released when the anther is grasped or pressed by the legs of an insect. Robertson (1929) considered the flower of *S. angularis* to be a "non-social long-tongued bee flower."

Floral records of bees (Mitchell, 1960; 1962) indicate that the species reported here are polylectic. They are known to gather pollen from a variety of plant groups, not exclusively from *Sabatia*. As opposed to oligolectic bees which visit specific plant groups for pollen, polylectic bees often are nectar-seeking (Raven, 1962) and will visit younger flowers with dehiscing anthers as well as older flowers which have receptive stigmata.

CHROMOSOME NUMBERS

The first chromosome numbers in *Sabatia* were published by Lewis, Stripling, and Ross (1962) who reported counts for *S. campestris* of $n=13$ (Brazos Co., Texas) and $2n=26$ (Nacogdoches Co., Texas). Bostick (1965) reported $n=14$ for *S. brachiata* (Pender Co., N.C.). Over 70 populations have now been sampled and chromosome counts made for all species in the genus.

Chromosome numbers were determined from buds collected in the field or from plants grown in a greenhouse. Counts were made from pollen mother cell preparations at metaphase I of meiosis. No report is based on an average or on a single observation. Buds were fixed in acetic alcohol (1:3) or in acetic alcohol chloroform (1:3:6); the addition of chloroform was found to enhance cytoplasmic staining and was discontinued. Buds collected from greenhouse material were placed in the fixative and refrigerated for 12 hours. The buds then were rinsed and stored in 70% ethanol under refrigeration. Field collections were refrigerated as soon as possible. Staining was done with acetocarmine. Most species presented no staining difficulties,

but *S. kennedyana* chromosomes usually were not very selectively stained with the standard techniques.

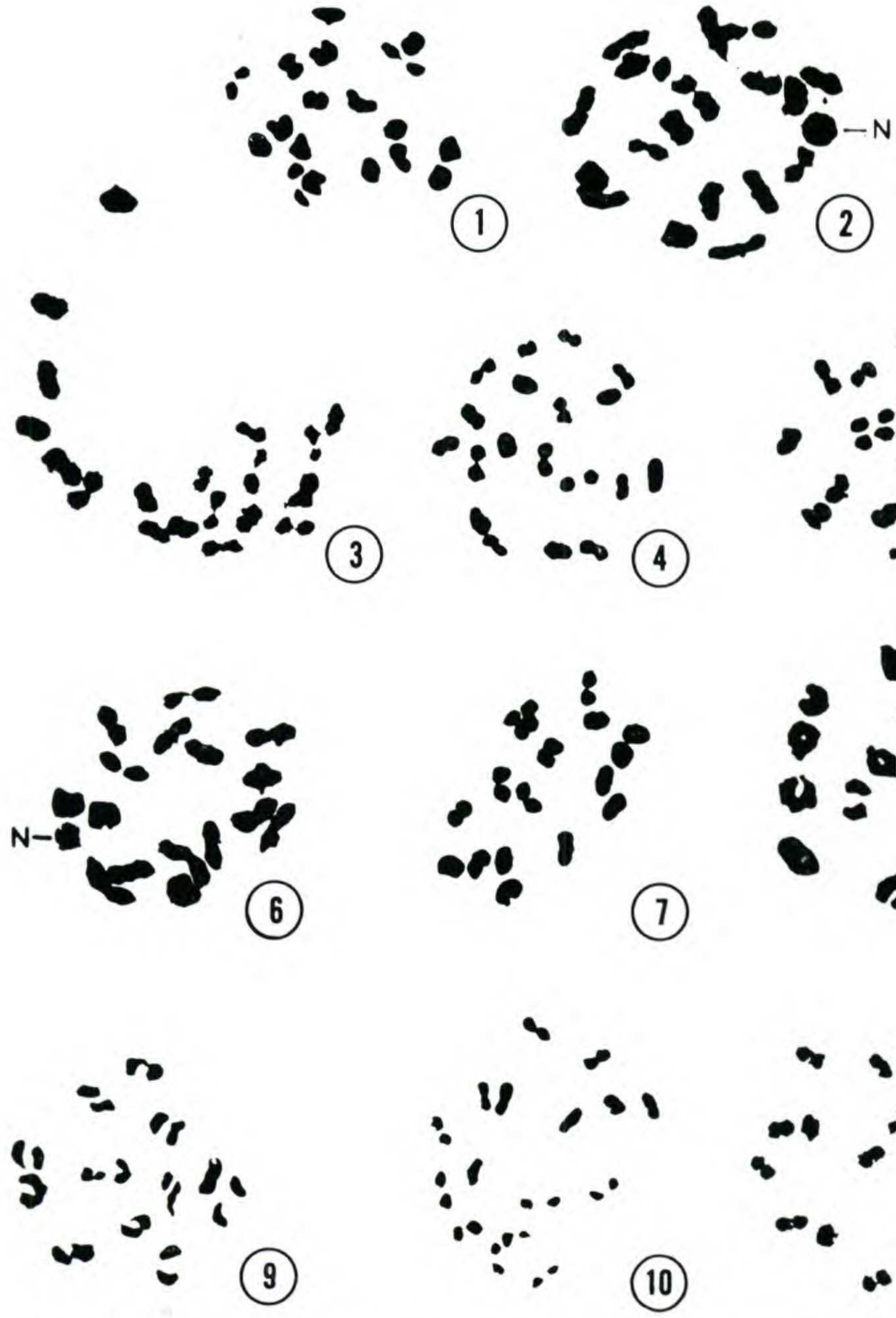
The hour of the day at which buds were fixed had no noticeable effect on the number of metaphase I figures observed. Buds ordinarily were collected from greenhouse material between the hours of 7:00 and 11:00 A.M. There is a correlation between anther size and developmental stage of the pollen tetrad although this varied somewhat with time of year and the individual plant's vigor. The five anthers of pentapetalous species had synchronous meiotic divisions. In pluripetalous species having 8 or more anthers, tetrad development was successive from anther to anther rather than simultaneous.

All observations and photographs were made from freshly stained preparations. Photographs were taken at ×1500 with a Leitz Ortholux microscope (90X objective, N.A. 1.32, 10× ocular) and Kodak Contrast Process Ortho film. Photographs were reduced to ×1000 for publication. Voucher specimens are deposited in the Duke University Herbarium.

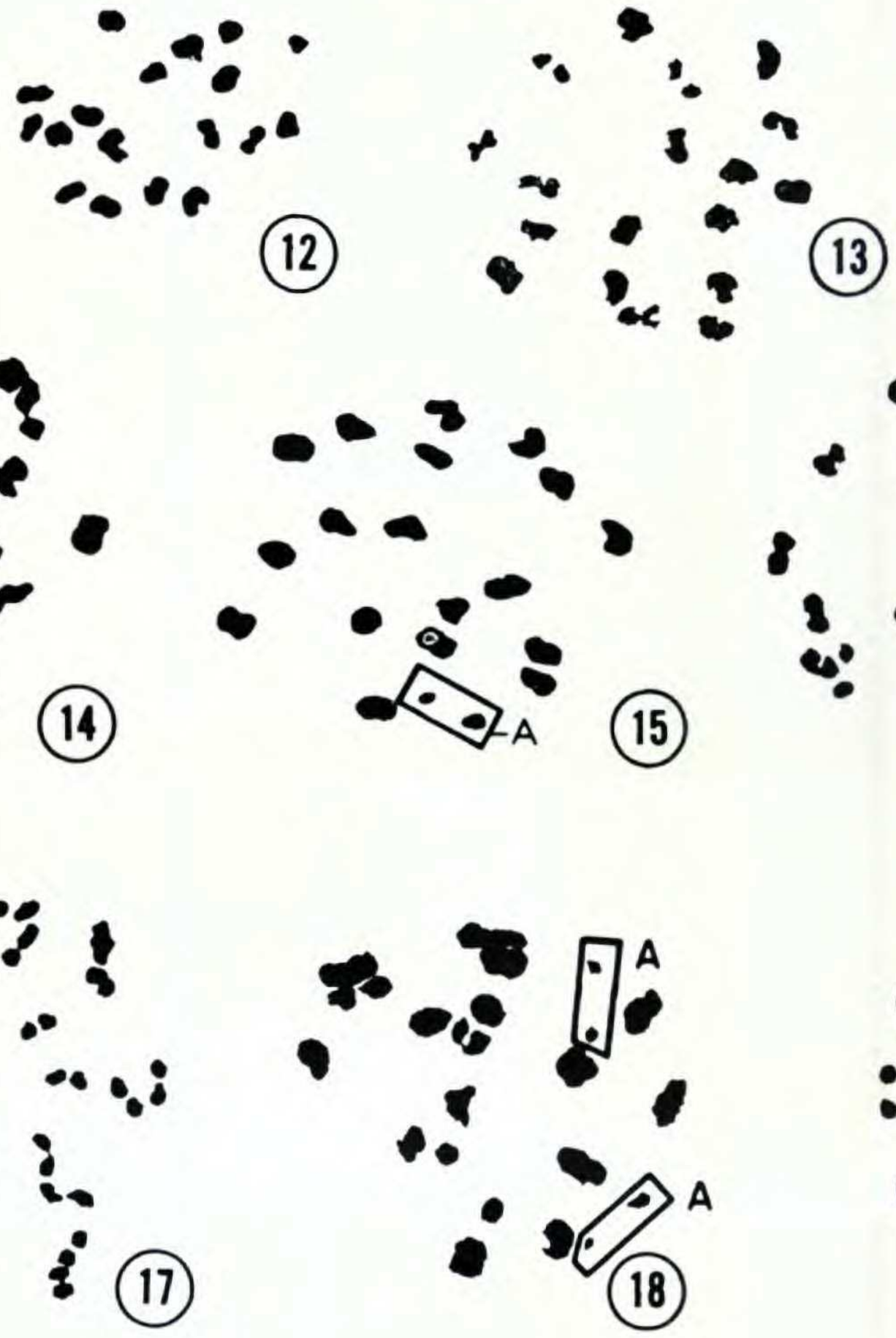
The count of $n=13$ for *S. campestris* (Lewis et al., 1962) was confirmed. My findings for *S. brachiata* ($n=16$), based on six individuals from two populations, do not agree with the n=14 count by Bostick (1965). Both reports are based on samples from the same county; such variation seems unlikely but not impossible. As a result of the present study a wide array of chromosome numbers for the genus is now known: $n=13$, 14, 16, 17, 18, 19, 20, 32, and 38. Various morphological types have developed at the different ploidal levels; in addition, two aneuploid races are known in a single species, *S. quadrangula* ($n=16$, 17). Some gametic complements are pictured in Fig. 1-22, and counts are summarized below. Collection numbers are mine unless otherwise specified.

S. difformis ($n=18$). **N.C.:** BRUNSWICK CO., 1 mi S of Longwood, 1293. 8 mi W of Leland, 1298. PENDER CO., 1 mi N of Watha, 1881. **S.C.:** JASPER CO., N of Grays, 1690. **Fla.:** SANTA ROSA CO., E Bank of Blackwater River at Milton, 1665.

S. macrophylla var. *macrophylla* ($n=19$). **Fla.:** SANTA ROSA CO.,



Figs. 1-11. Meiotic chromosomes of *Sabatia*. ×1000. Fig. 1. *S. difformis, Perry* 1881, *n*=18. Fig. 2. *S. macrophylla* var. *macrophylla, Perry* 1449, *n*=19 (nucleolus, N). Fig. 3. *S. macrophylla* var. *recurvans, Perry* 1650, *n*=19. Fig. 4. *S. angularis, Perry* 1303, *n*=19. Fig. 5. *S. brachiata, Perry* 1884, *n*=16. Fig. 6. *S. quadrangula, Perry* 1655, *n*=16 (nucleolus, N). Fig. 7. *S. quadrangula, Perry* 1655, *n*=16 (nucleolus, N). Fig. 7. S. *quadrangula Perry* 1455, *n*=17. Fig. 8. *S. arenicola, Perry* 1425, *n*=14. Fig. 9. *S. campestris, Perry* 1429, *n*=13. Fig. 10. *S. brevifolia, Perry* 1696, *n*=16. Fig. 11. *S. campanulata, Perry* 1391, *n*=17.



Figs. 12-22. Meiotic chromosomes of *Sabatia*. ×1000. Fig. 12. *S. grandiflora, Stone* 1671, *n*=18. Fig. 13. "*S. simulata*," *Perry* 1637, *n*=18. Fig. 14. S. *stellaris, Perry* 1294, *n*=18. Fig. 15. *S. stellaris, Perry* 1517, *n*=18 (accessory chromosomes, A). Fig. 16. *S. bartramii, Perry* 1443, *n*=18. Fig. 17. *S. calycina, Stone* 1648, *n*=32. Fig. 18. *S. dodecandra* var. *dodecandra, Wilbur* 8475, *n*=17 (accessory chromosomes, A). Fig. 19. *S. dodecandra* var. *foliosa, Perry* 1678, *n*=19. Fig. 20. *S. kennedyana,* Perry 1694, n=20. Fig. 21. *S. capitata, Perry* 1661, *n*=38. Fig. 22. *S. gentianoides, Perry* 1670, *n*=14.

10.5 mi N of Holley, 1449. **Miss.**: STONE CO., Univ. of Miss. forestry camp, 1389.

S. macrophylla var. *recurvans* (*n*=19). **Ga.**: CHARLTON CO., 12 mi S of Folkston, 1650, **Fla.**: COLUMBIA CO., 5.4 mi W of Olustee, 1685.

S. angularis (*n*=19). **N.C.**: DURHAM CO., 2.4 mi E of Catsburg, 1303. **Ga.**: OGLETHORPE CO., 16 mi NE of Lexington, 1890. **Md.**: CALVERT CO., 1 mi W of Chesapeake Beach, 2021.

S. quadrangula (*n*=16, 17). **N.C.**: DURHAM CO., 2.2 mi E of Catsburg, 1655 (*n*=16). **Ga.**: WALTON CO., Anglin Farm granite outcrop, 1886 (*n*=17). **Fla.**: CALHOUN CO., 1.4 mi E of Clarksville, 1455 (*n*=17).

S. brachiata (*n*=16). **N.C.**: PENDER CO., 3 mi S of Burgaw, 1300. 4 mi S of Burgaw, 1884.

S. campestris (*n*=13). **Texas**: HARDIN CO., S of Sour Lake, 1429.

S. arenicola (*n*=14). **Texas**: GALVESTON CO., Jamaica Beach, S of Galveston, 1425. Galveston Beach, 1427.

S. *campanulata* (*n*=17). **Tenn.**: CARTER CO., Hunter Bog at Hunter, E of Elizabethton, 1659. **N.C.**: PENDER CO., 1 mi N of Watha, 1882. **Ga.**: BARTOW CO., 4.5 mi SE of Adairsville, 1663. **Fla.**: COLUMBIA CO., 7.8 mi W of Olustee, 1684. **Miss.**: STONE CO., Univ. of Miss. forestry camp, 1391.

S. stellaris (n=18; including "*S. simulata*" from Bahamas). **N.C.**: BRUNSWICK CO., Caswell Beach, 1294. CARTERET CO., Shackleford Bank, 1478. DARE CO., Outer Banks, near road to Manteo, 1656. **Fla.**: BROWARD CO., W of Deerfield, 1567. COLLIER CO., 7.1 mi E of Monroe Station, 1517. TAYLOR CO., N edge of Aucilla Wildlife Management Area, *B. J. Moore, s.n.* **Eleuthera Island**: N end, E of Current, 2038. S end, N of Davis Harbour, 2040. NE of Preacher's Cave, 2043. **Great Abaco Island**: SW of Marsh Harbour near pulpwood plant, 1777. SW of Marsh Harbour, 1779. In "whitelands" 3 mi W of Owens-Illinois pulpwood plant, 1784. NW of Marsh Harbour, toward Green Turtle Cay, 1799. **New Providence Island:** marsh S of Carmichael Village, S coast, 1637.

S. grandiflora (*n*=18). **Fla.**: BAY CO., SE shore of Lake Merial, *D. E. Stone* 1452. COLLIER CO., Everglades, N of Loop Road at Pinecrest, 1555. HIGHLANDS CO., W of Kissimmee River along Fla. route 70, *D. E. Stone* 1671. LAKE CO., W of Sorrento, 1682.

S. brevifolia (*n*=16). **S.C.**: COLLETON CO., 3 mi W of Smoaks, 1696. **Fla.**: COLLIER CO., 7.5 mi NW of Immokalee, *O. Lakela* 30216. HILLSBOROUGH CO., Univ. of South Florida campus, *R. W.* and *K. Long* 2013. LEVY CO., between Bronson and Otter Creek, *B. J. Moore s.n.* SUMTER CO., between Rutland and Wildwood, *B. J. Moore s.n.*

S. calycina (*n*=32). **N.C.**: BRUNSWICK CO., SW of Wilmington, 1296. **Fla.**: COLLIER CO., W of Collier Co. Scenic Rd., 1539. OSCEOLA CO., 0.5 mi W of Brevard Co.-Osceola Co. line, *D. E. Stone* 1648.

S. dodecandra var. *dodecandra* (n=17 + 4 accessory chromo-

somes). **N.C.:** CARTERET CO., 13 mi N of Beaufort toward South River, 1885. *R. L. Wilbur* 8475.

S. dodecandra var. *foliosa* (*n*=19). **S.C.:** JASPER CO., 5.4 mi S of Ridgeland, 1689. **Ga.:** ATKINSON CO., 14 mi S of Pearson, *S. A. Earle* 65112. **Fla.:** HAMILTON CO., E of Jasper, 1683. JEFFERSON CO., 2.3 mi W of Lamont, 1458. LAFAYETTE CO., Steinhatchee Wildlife Management Area, 1678. SANTO ROSA CO., E bank of Blackwater River at Milton, 1666.

S. *kennedyana* (*n*=20). **Mass.:** BARNSTABLE CO., E bank of Cedar Lake, Cape Cod, 1694. **S.C.:** HORRY CO., just E of Waccamaw River, 1875.

S. bartramii (*n*=18). **Ga.:** CHARLTON CO., 3.4 mi S of St. George, 1687. **Fla.:** BAY CO., 5 mi E of Panama City, 1672. COLLIER CO., 7 mi E of Monroe Station, 1521. HERNANDO CO., 1 mi NW of Aripeka, 1679. LEVY CO., N of Cedar Key, *B. J. Moore s.n.* SANTA ROSA CO., 10.5 mi N of Holley, 1446. WAKULLA CO., SE of Wakulla, 1675. **Ala.:** BALDWIN CO., 0.7 mi NE of Stapleton, 1443.

S. capitata (*n*=38). **Ga.:** WALKER CO., Pigeon Mt., SW of Lafayette, 1661.

S. gentianoides (*n*=14). **Ga.:** CHARLTON CO., 8.3 mi N of St. George, 1688. **Fla.:** WALTON CO., 1.5 mi N of Choctawhatchee Bay, 1670.

Few meiotic irregularities were observed. Chromosomes of *S. dodecandra* var. *dodecandra* and of *S. brachiata* occasionally showed early disjunction. Accessory chromosomes were seen in preparations from one collection of *S. stellaris* from Florida (*Perry* 1517, Fig. 15). Of 50 cells studied from this population, 78% had one or two accessory chromosomes. Only one population of *S. dodecandra* var. *dodecandra* was available for study. Four accessory chromosomes were consistently associated with the 17 pairs in all cells studied (Fig. 18). It is uncertain whether the original number was *n*=19 (as in *S. dodecandra* var. *foliosa*), and the essential parts of the accessory have been transferred to other chromosomes through translocation, or whether this was a local aberrant population and the usual number is *n*=19. Other collections of the variety must be made for further study.

As the haploid chromosome number decreases in *Sabatia* there is a tendency toward the annual or biennial habit and a corresponding simplification of morphology. There is a decrease in floral size, number of floral parts, and promi-

nence of leaves. Most of the annuals and biennials are capable of growing in drier habitats. In one annual species (*S. arenicola*, $n=14$) an inbreeding system has been derived as an additional specialization for the annual growth habit. Similar correlations with descending aneuploidy have been recorded in the literature for several genera in other families and, in the Gentianaceae, for *Swertia* (Khoshoo and Tandon, 1963).

POLLEN VARIATION

There appear to be no differences in exine sculpturing among the species. The exine has a granular texture and the wall is about 1.0-2.5 μ thick. The grains are tricolpate and each colpus has a circular germ pore. The aperture membrane is smooth and sometimes protrudes beyond the general outline. In polar view the grains are triangular with rounded apices.

Pollen samples were taken from 88 live plants of 49 populations. Pollen was placed directly in lactophenol-cotton blue; measurements were made about 24 hours after collection. The grains usually were oriented in polar view on the slide. Therefore, all measurements were made from one pore past the polar axis to the wall opposite the pore. Grains distorted or with unequal planes of symmetry in polar orientation were not measured. A Spencer microscope with 10× oculars and 44× objective was used for measurements which were made to the nearest optical line (1 division = 1.52 μ).

Since many of these individuals were used in the experimental hybridizations, it was necessary to obtain pollen fertility data in order to establish expected norms of fertility in parental species. Fertility estimates are based on the number of stained grains in a sample of not less than 400 grains from each species.

Combined results of the pollen size measurements and fertility estimates are given in Table 2. There are no consistent correlations of pollen size with chromosome number. Those species with 13 or 14 pairs of chromosomes have grains which are fully as large as grains of species with a

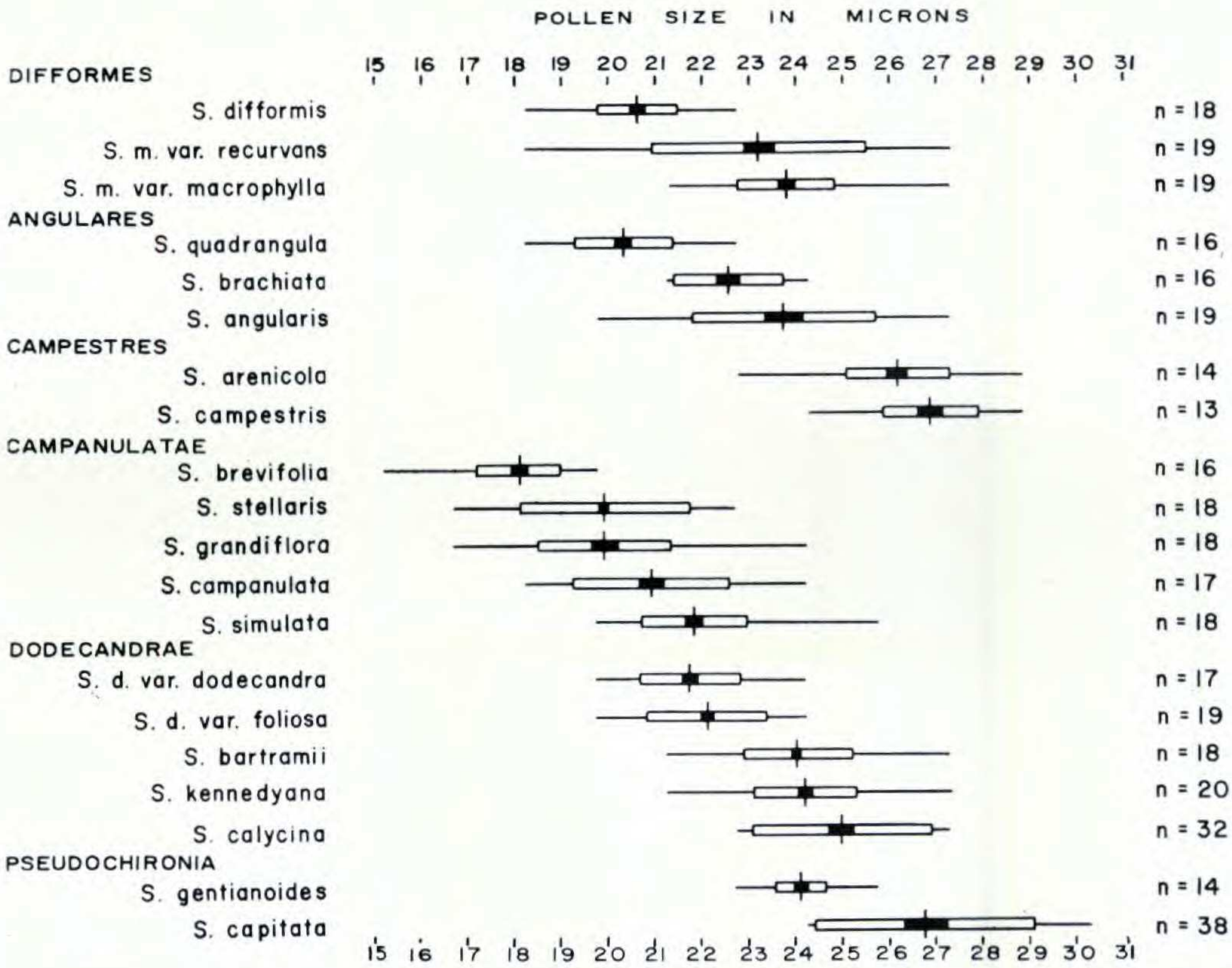


Fig. 23. Pollen size in *Sabatia*. The length of each line represents the range of that set of measurements. A crossbar shows the position of the mean; on each side of the mean the dark line marks two times the standard error and the open rectangle extends for one standard deviation.

higher number of 18 or more pairs. With regard to ranges of means, there seems to be a tendency for members of each subsection to be grouped more closely with one another than with other subsections (Fig. 23). Nonetheless, pollen size is unreliable as an indicator of ploidy and is not useful as a species characteristic.

EXPERIMENTAL HYBRIDIZATIONS

There are no published accounts of either artificial or natural interspecific hybridizations in *Sabatia*. The artificial pollinations reported here were done under similar cultural conditions during two growing seasons. Reciprocal crosses were made among almost all taxa, and an attempt was made to repeat each crossing combination at least ten times using plants from different populations.

TABLE 2

Size and fertility estimates of *Sabatia* pollen (SE, standard error of mean; SD, standard deviation of mean; CV, coefficient of variation).

Taxa	Size in μ		SE	SD	CV	Number Grains Measured	Percent Viable	Number Grains Scored
	Range	Mean						
Section *Sabatia*								
Subsect. *Difformes*								
S. difformis	18.21 - 22.76	20.59	.07	0.85	.04	150	94.6	1400
S. m. var. *macrophylla*	21.25 - 27.32	23.80	.09	1.04	.04	150	97.0	1200
S. m. var. *recurvans*	18.21 - 27.32	23.20	.16	2.29	.10	200	94.2	1400
Subsect. *Angulares*								
S. angularis	19.73 - 27.32	23.75	.20	1.96	.08	100	95.5	900
S. quadrangula	18.21 - 22.76	20.29	.08	1.07	.05	200	92.7	1600
S. brachiata	21.25 - 24.28	22.58	.12	1.17	.05	100	95.7	1200
Subsect. *Campestres*								
S. campestris	24.28 - 28.83	26.89	.14	1.02	.04	50	98.4	500
S. arenicola	22.76 - 28.83	26.21	.11	1.10	.04	100	95.1	800

Subsect. *Campanulatae*								
S. campanulata	18.21 - 24.28	20.93	.14	1.70	.08	150	97.8	400
S. stellaris	16.70 - 22.76	19.94	.05	1.82	.07	650	95.8	5100
"*S. simulata*"	19.73 - 25.80	21.84	.08	1.16	.05	200	93.7	1400
S. grandiflora	16.70 - 24.28	19.95	.12	1.42	.07	150	95.9	900
S. brevifolia	15.18 - 19.73	18.12	.09	0.89	.05	100	96.8	1000
Subsect. *Dodecandrae*								
S. calycina	22.76 - 27.32	25.02	.14	1.97	.08	200	97.4	1600
S. d. var. *dodecandra*	19.73 - 24.28	21.76	.09	1.11	.05	150	97.2	900
S. d. var. *foliosa*	19.73 - 24.28	22.13	.07	1.30	.06	300	95.0	2100
S. kennedyana	21.25 - 27.32	24.24	.07	1.10	.05	250	93.2	2000
S. bartramii	21.25 - 27.32	24.06	.05	1.19	.05	475	96.7	3000
Section *Pseudochironia*								
S. capitata	24.28 - 30.35	26.80	.24	2.35	.09	100	98.5	800
S. gentianoides	22.76 - 25.80	24.13	.08	0.56	.02	50	95.5	400

Approximately 4400 pollinations have been recorded.

Emasculation was accomplished by removing stamens before the stigmatic branches became untwisted and receptive. In *S. arenicola* and *S. calycina* this necessitated opening the flower bud. Removal of petals had no effect on subsequent ovary or seed development. Mature anthers were detached with forceps and used as applicators of pollen to the emasculated female parent.

Foreign pollen was excluded by screening the greenhouse and by enclosing emasculated flowers in glassine envelopes. As a check of contamination, flowers were emasculated as usual and not artificially pollinated. Capsules were examined later for seed set. Fertility controls were maintained by frequent checks of pollen viability and by selfing. Interpopulational crosses gave the same results as those obtained from self-pollinations. As measured by pollen viability and seed set, fertility of all parental plants was high. In no case, however, were the last flowers of a season used in the crossing program.

Ease of crossing may be estimated from the number of hybrid seeds taken from a given number of emasculated and cross-pollinated flowers (Grant and Grant, 1960). Each cross was evaluated in terms of the average number of ovules tested in the female parent. This procedure has proved useful in a number of studies (*see* Borrill, 1958; Ellison, 1964; Taylor, 1965) and was modified from Gillett (1955) and Levin (1966) for use with *Sabatia*. The number of ovules tested was obtained by averaging the number of seeds produced by ten or more self-pollinated flowers of the female parent. It is assumed that, when a flower is selfed with liberal amounts of pollen, the number of seeds released will be equivalent to the number of ovules normally produced by that species. Percentage seed set was derived by dividing the total number of filled seeds obtained in a given series of crosses by the number of ovules tested in the same number of crosses.

Crossability, as used here, means the extent to which hybrid seeds are formed. It is expressed as a percentage of the average ovule production of the pistillate parent.

Since the germination of non-hybrid *Sabatia* seed varies with storage conditions, specific germination percentages for hybrids are not used as a measure of crossability. Relative germinability, however, has been useful in evaluating the crosses. Samples of seed from each crossing combination were sown to verify viability.

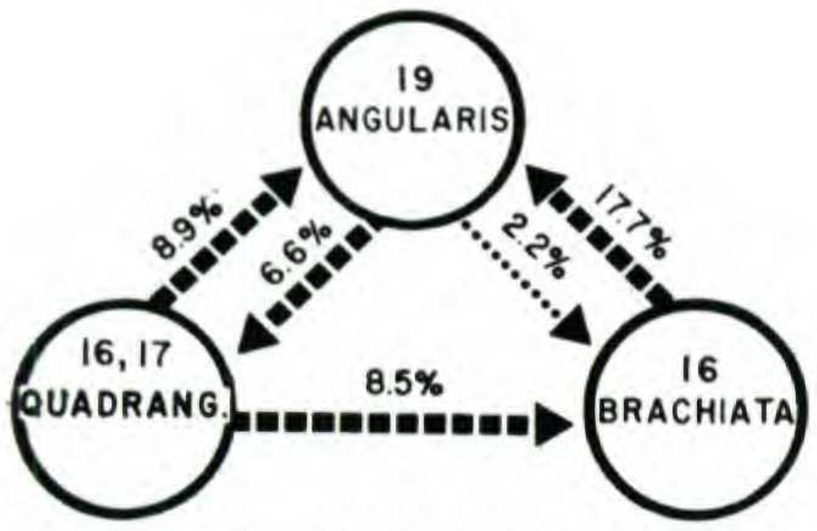
The success of crosses, in terms of crossability and interfertility, serves as a test of the validity of taxonomic groupings (Kruckeberg, 1961). In addition, crossability elucidates genetic relationships of the parental species. Lowered crossability may mean a more distant genetic relationship, although the action of a few genes can obscure this (Khush, 1962). Thus, while inability to cross may be at times an unsafe guide to relationship, the use of crossability in the positive sense is not unreliable (Valentine, 1961).

Intrasubsectional and intrasectional crosses in *Sabatia* are summarized in Fig. 24. Lines graphically present the seed set percentage, and the actual value is given for successful crosses. All successful crosses within the genus are shown in Fig. 25. A complete listing is presented in Perry (1967).

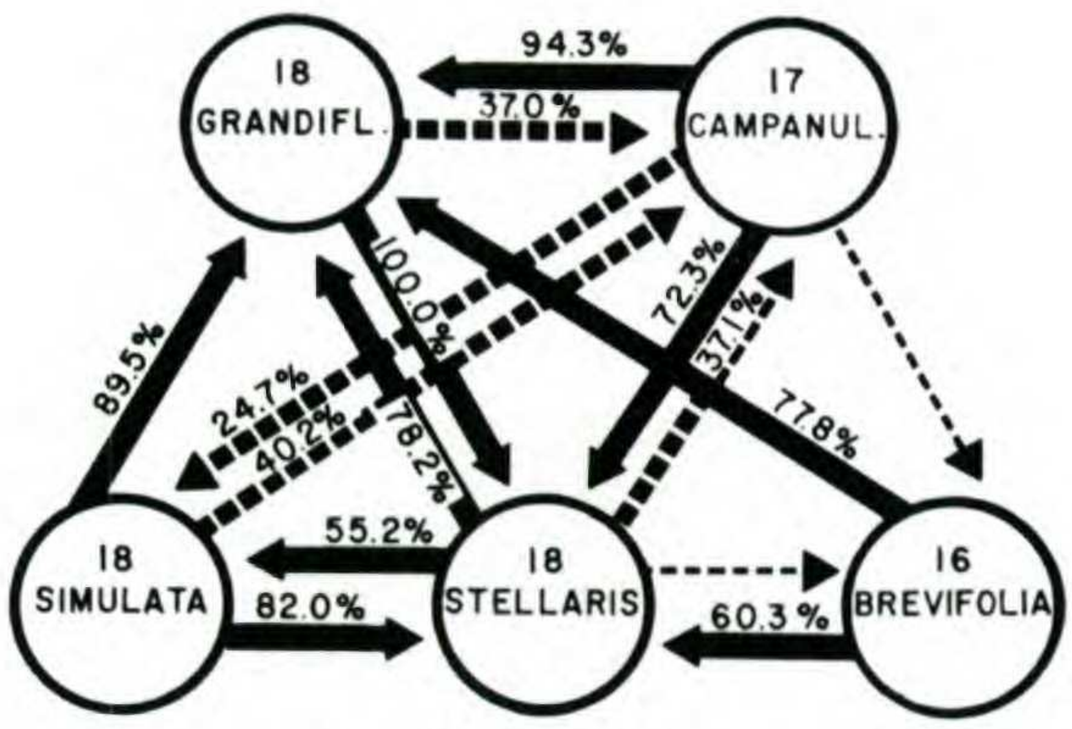
1. CROSSES WITHIN SUBSECTIONS OF SECTION SABATIA.

Subsect. DIFFORMES. There is unequal reciprocal crossability between *S. macrophylla* and *S. difformis*. Seed set is reduced when *S. difformis* is used as the pollen parent to either variety of *S. macrophylla*. Differences in style lengths do not account for the discrepancy since the style of *S. macrophylla* is shorter than that of *S. difformis*. Hybrid seeds germinated well but, due to cultural difficulty, no hybrids reached maturity.

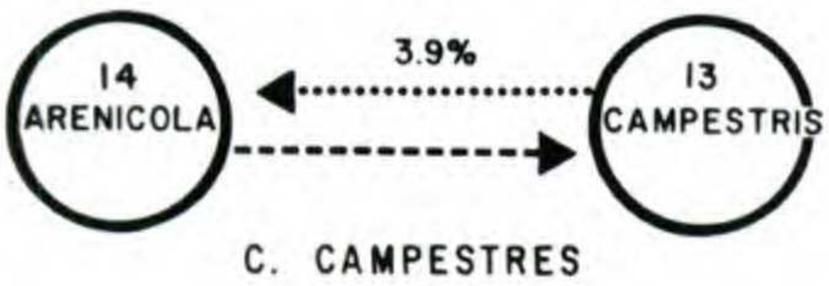
Subsect. ANGULARES. Members of *Angulares* have only slight crossability. The n=16 race of *S. quadrangula* showed greater crossing compatibility with *S. angularis* than did the n=17 race. This accounts for the higher value of 8.9% in the *S. angularis* (♀) × *S. quadrangula* crosses in which the n=16 race was incorporated. In the reciprocal, only the n=17 race was used. The n=17 race was used



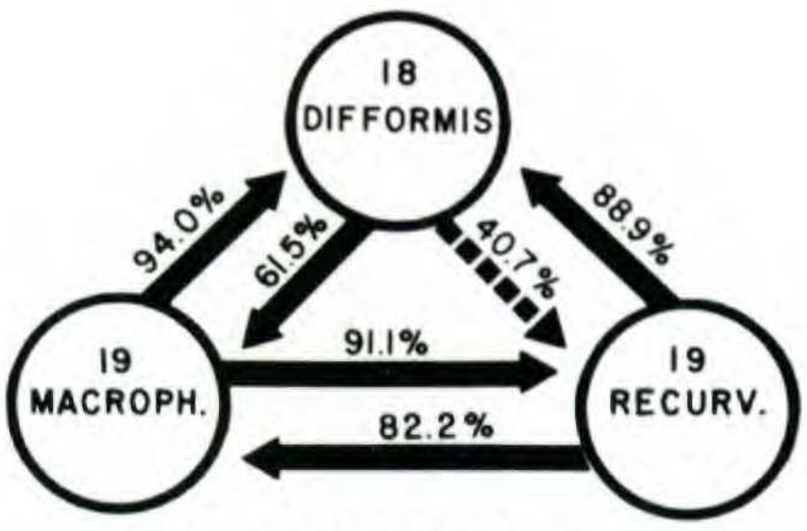
A. ANGULARES



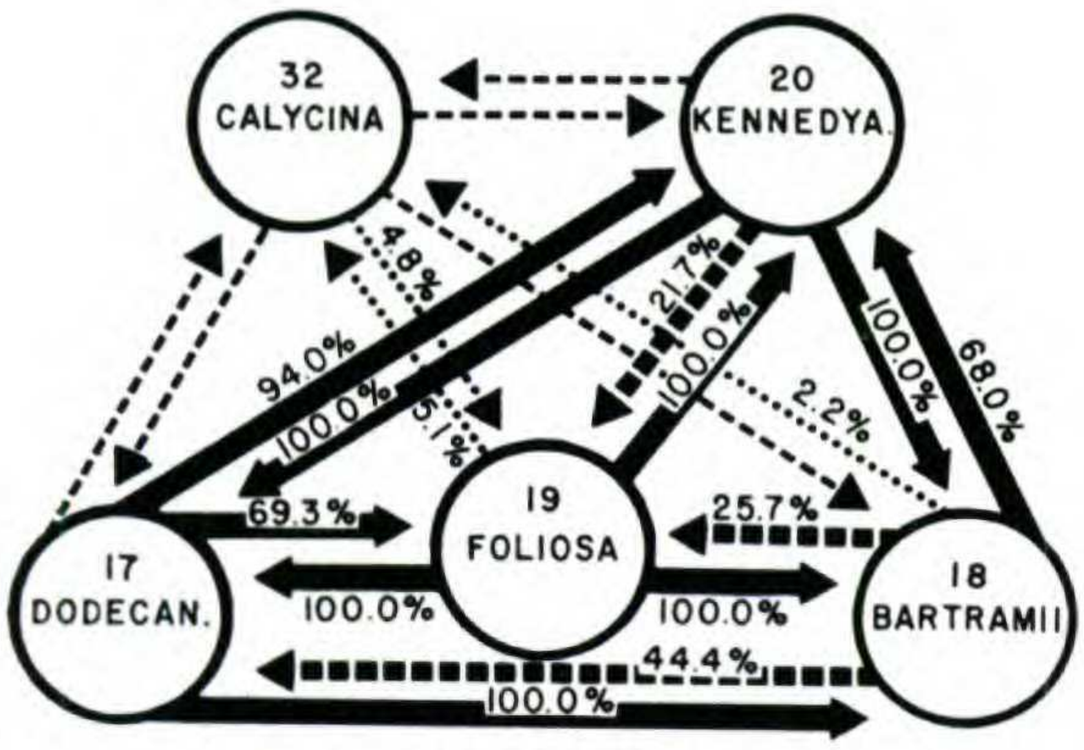
B. CAMPANULATAE



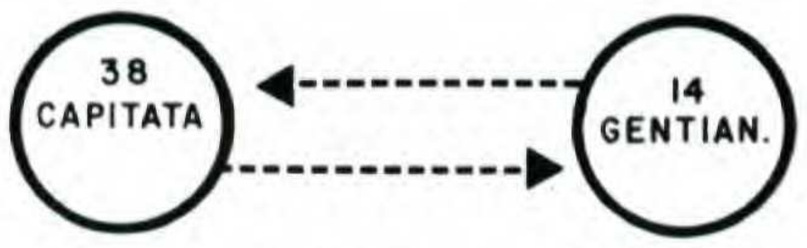
C. CAMPESTRES



D. DIFFORMES



E. DODECANDRAE



F. PSEUDOCHIRONIA

♂→♀

SEED SET 51-100%
SEED SET 1-50%
SEED SET SPORADIC
NO SEEDS PRODUCED

Fig. 24. Crosses within subsections of Section *Sabatia* and within Section *Pseudochironia*. Percentage seed set is given for successful crosses. The gametic chromosome number of each taxon is indicated. A. Crosses among members of Subsect. *Angulares*. B. Crosses among members of Subsect. *Campanulatae*. C. Crosses between members of Subsect. *Campestres*. D. Crosses among members of Subsect. *Difformes*. E. Crosses among members of Subsect. *Dodecandrae*. F. Crosses between members of Section *Pseudochironia*.

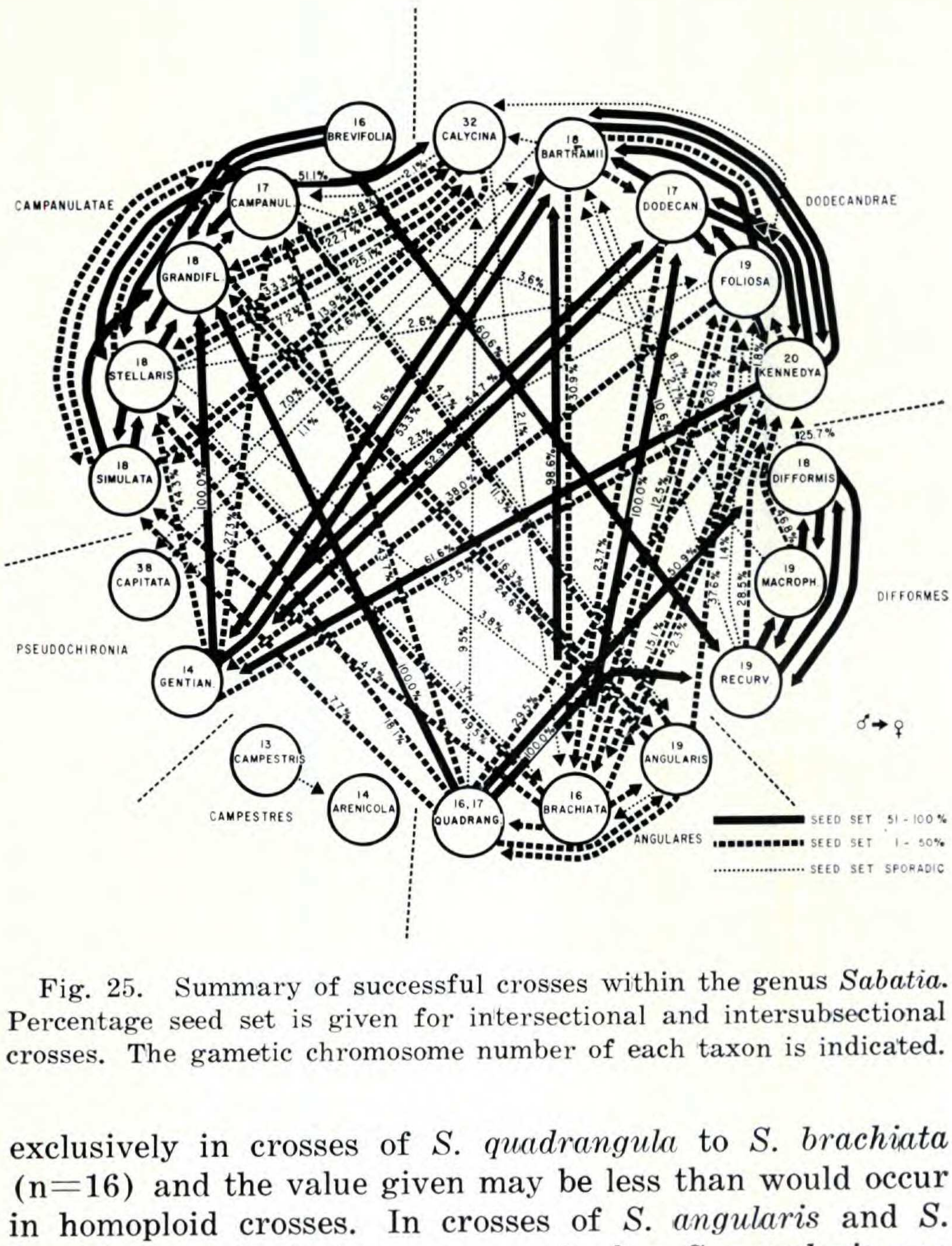


Fig. 25. Summary of successful crosses within the genus *Sabatia*. Percentage seed set is given for intersectional and intersubsectional crosses. The gametic chromosome number of each taxon is indicated.

exclusively in crosses of *S. quadrangula* to *S. brachiata* (n=16) and the value given may be less than would occur in homoploid crosses. In crosses of *S. angularis* and *S. brachiata*, seed set always occurred when *S. angularis* was the pistillate parent. Only one of five crosses resulted in seed set when *S. angularis* was the pollen parent, thus the value of 2.2% does not give positive evidence of crossability. Hybrids were unhealthy and did not reach reproductive maturity.

Subsect. CAMPESTRES. Although 62 attempts were made,

Campestres and *Difformes*, *Campanulatae*, *Dodecandrae*, or *Angulares*.

ANGULARES × DIFFORMES. *Sabatia quadrangula* was found to cross readily as the pollen parent with *S. difformis* and *S. macrophylla* var. *recurvans*, but hybrids did not mature. The reciprocal crosses were not made due to a lack of material of *S. quadrangula*, and no crosses of *S. quadrangula* were made to *S. macrophylla* var. *macrophylla*. Other species of the *Angulares* failed to cross with members of *Difformes*.

CAMPANULATAE × DIFFORMES. *Sabatia brevifolia* as the pollen parent crossed with *S. macrophylla* var. *recurvans*. The former species was not available for additional crosses because of its late flowering. All other crosses failed.

ANGULARES × DODECANDRAE. There was moderate to high crossability of *S. brachiata* with *S. dodecandra* var. *dodecandra* (no hybrid grown), *S. kennedyana* (no hybrid), *S. bartramii* (hybrid sterile; see Table 3), and *S. dodecandra* var. *foliosa* (hybrid fertility low).

Sabatia quadrangula crossed only as the pollen parent with *S. calycina* and *S. kennedyana*. *Sabatia angularis* crossed as the pollen parent with *S. dodecandra* var. *foliosa*.

DODECANDRAE × DIFFORMES. Only *S. kennedyana* crossed as the seed parent with members of the *Difformes*: *S. difformis* and *S. macrophylla* vars. *macrophylla* and *recurvans*. The hybrids from these three crosses were sterile. They resembled the pollen parents by having tightly coiled stigmas and white flowers, but incorporated the yellow floral "eye," larger flower, and increased petal number of the seed parent. The reciprocal crosses gave no positive evidence of crossability. Members of *Difformes* showed slight crossability to *S. dodecandra* var. *foliosa* and to *S. bartramii*.

CAMPANULATAE × ANGULARES. Pollen from each species of the *Angulares* produced seed when crossed with one or more members of the *Campanulatae*. As a seed parent, only *S. angularis* crossed with members of *Campanulatae*. *Sabatia brachiata* crossed exclusively with *S. stellaris*.

The F_1 hybrids from the cross of *S. stellaris* (♀) × *S.*

brachiata were sterile. Of 1300 pollen grains scored from four plants, 1.3% were viable; three of the four plants had no viable pollen. The hybrids were similar in morphology to the pistillate parent.

Hybrids from the cross of *S. stellaris* (♀) × *S. quadrangula* are also available (Table 3). The hybrids had white corolla lobes tinged with pink on the underside. The petals were rather broadly spatulate and the yellow floral "eye" of *S. stellaris* was present. In addition to having white corollas, the hybrids resembled the pollen parent by having opposite branches, broad leaves, and an angular stem. The calyx lobes usually exceeded those of the corolla.

Hybrids of *S. grandiflora* (♀) and *S. campanulata* (♀) with *S. angularis* were not vigorous. Vegetatively they resembled the pistillate parent.

DODECANDRAE × CAMPANULATAE. It is significant that only *S. calycina (Dodecandrae)* crossed freely with all members of the *Campanulatae* except *S. brevifolia*. *Sabatia kennedyana* possibly crossed with *S. campanulata*, although the percentage is so low as to be unreliable. *Sabatia bartramii* and *S. dodecandra* var. *foliosa* crossed infrequently with *S. stellaris*.

Vigorous hybrids resulted from reciprocal crosses of *S. stellaris* and *S. calycina*. There was little variability among the 239 F_1 individuals grown. Hybrids had the large ovary, broad leaves, prominent nodes, and foliose calyx lobes of *S. calycina*. Calyx lobes ordinarily exceeded in length those of the corolla. With *S. stellaris* as the pollen parent, five corolla and calyx lobes characterized the hybrids; when *S. calycina* was the pollen donor six lobes were characteristic. Stained pollen grains often were 4-colpate.

Other hybrids of *S. calycina* with *S. campanulata* and *S. grandiflora* have been grown (Table 3). They clearly incorporated traits of both parents and were largely sterile.

4. CROSSES BETWEEN SECTIONS SABATIA AND PSEUDOCHIRONIA.

Sabatia capitata (Pseudochironia) crossed as the pistillate parent with *S. bartramii* and *S. dodecandra* var. *foliosa*

(Sabatia: Dodecandrae). Only the reciprocal cross with *S. bartramii* as the pistillate parent was occasionally successful.

Sabatia gentianoides (Pseudochronia) crossed with all members of the *Dodecandrae* except *S. calycina*. Only the reciprocal cross using *S. dodecandra* var. *foliosa* as the pistillate parent failed. *Sabatia gentianoides* pollen also effected fertilization in *S. campanulata*, *S. grandiflora*, and *S. stellaris (Sabatia: Campanulatae)*. The reciprocal crosses failed.

Hybrid seed germinability was good. One cross is available for analysis at the present time (Table 3). The hybrids of *S. gentianoides* (♀) × *S. bartramii* were intermediate in vegetative morphology between the parental species. While *S. gentianoides* always has prominent bracts subtending the flowers, the hybrid does not. The number of calyx and corolla lobes was reduced often to 9, but ranged to 12.

SYMPATRY AND ISOLATING BARRIERS

The differentiation of species in *Sabatia* has been accompanied by changes in chromosome number. These changes, which in part reduce or prohibit crossability, are coupled with other isolating barriers. As a result, natural interspecific hybridization is unknown.

A series of 14 extensive field trips during three growing seasons has permitted observations of naturally occurring populations of each species. All sympatric occurrences of species were recorded. As many as five species have been found growing sympatrically, and ten sympatric combinations were noted. In almost every case the species were distributed according to differences in microhabitat. This characteristically non-random distribution was observed in New Jersey by Stone (1908) who wrote: "The curious transition in floras as one approaches the salt water from the pine barrens was beautifully shown about Cold Spring, especially by the *Sabbatias* [sic]. Back at the head of the swamp in a little tract of pine barren affinities, grew the white *S. lanceolata* [= *S. difformis*], which gave way along

TABLE 3

Pollen fertility of F_1 interspecific hybrids in *Sabatia*. The pistillate parent is given first in each hybrid combination.

Hybrid Combination	Percent Stainable Pollen Mean	Pollen Range	Grains Scored	Number Plants
Campanulatae × Campanulatae				
campanulata × grandiflora	44.7	—	1000	1
campanulata × stellaris	8.8	0 - 29.5	1300	6
grandiflora × brevifolia	0	—	300	1
grandiflora × stellaris	0	—	1500	3
stellaris × brevifolia	37.4	—	500	1
stellaris × campanulata	13.5	1.5 - 29.0	1000	4
stellaris × campanulata	56.7	26.0 - 85.0	1200	5
stellaris × "simulata"	26.7	13.5 - 42.0	600	3
stellaris × "simulata"	96.3	88.0 - 99.3	5300	15
"simulata" × stellaris	74.8	37.0 - 95.0	1800	9
Dodecandrae × Dodecandrae				
bartramii × dodecandra var. foliosa	1.6	—	1000	1

(TABLE 3 — *continued*)

dodecandra var. dodecandra × bartramii	0.6	—	1000	1
dodecandra var. foliosa × calycina	10.8	—	1000	1
dodecandra var. foliosa × kennedyana	0	—	anthers aborted	1
Angulares × Dodecandrae				
brachiata × bartramii	0	—	500	1
brachiata × dodecandra var. foliosa	2.6	0 - 7.5	2825	15
dodecandra var. foliosa × angularis	36.6	—	500	1
Campanulatae × Angulares				
campanulata × angularis	52.5	44.7 - 61.6	3000	3
grandiflora × angularis	0	—	5000	4
stellaris × brachiata	1.3	0 - 3.4	1300	4
stellaris × quadrangula	2.6	0 - 5.8	1600	4
Campanulatae × Dodecandrae				
grandiflora × calycina	0	—	800	2
grandiflora × calycina	6.1	0.4 - 23.2	7000	4

stellaris × calycina	0.6	0 - 1.0	1000	3
stellaris × calycina	5.2	0 - 19.0	3000	8
calycina × stellaris	1.9	0 - 5.0	1500	3
Dodecandrae × Difformes				
difformis × kennedyana	0	—	2000	1
kennedyana × difformis	0	—	500	1
kennedyana × macrophylla var. macrophylla	0	—	1000	1
kennedyana × macrophylla var. recurvans	0	—	2000	4
Pseudochironia × Dodecandrae				
gentianoides × bartramii	0.6	0 - 1.2	4000	6

the coastal strip to *S. angularis*, which in turn was replaced by *S. stellaris* in the salt meadows."

The present study reveals that such species found to be sympatric are not intercrossable and belong to different supraspecific categories. Ornduff (1966) has suggested that related species which maintain genetic integrity when sympatric usually are sufficiently distinctive as to be placed in different supraspecific categories by a taxonomist. The only example in *Sabatia* of sympatry involving clearly crossable members of the same subsection was reported by Wilbur (1955). He found mixed herbarium sheets of *S. stellaris* and *S. grandiflora* indicating an overlap in habitats.

Most sympatric species of *Sabatia* differ in floral morphology, and insect visitors vary with the species. In addition, when there is a close aggregation of individuals of a single species, crossing within the population is more likely to occur than is hybridization with another, neighboring species. This massing of flowers of one form tends to discourage indiscriminate pollen transfer by insects into and out of the population (Baker, 1951). Individual species of *Sabatia* frequently are found growing in close stands in favorable situations.

Sabatia brevifolia is seasonally isolated. It flowers from September through mid-November in the southern part of its range. No other related species flowers at that time. *Sabatia kennedyana* is seasonally isolated, for the most part, in North and South Carolina. In New England and Canada it is ecologically and spatially isolated.

Sabatia capitata and *S. arenicola* are spatially isolated from other species in the genus. Strong inherent barriers to crossing exist also.

An inbreeding system further restricts hybridization. Autogamy and correlated morphological adaptations are found in *S. calycina* and *S. arenicola*.

The lack of natural hybrids in *Sabatia* shows the strength of these cytological, ecological, ethological, seasonal, and spatial isolating barriers. In the case of sympatric crossable species, such as *S. grandiflora* and *S. stellaris*, the fact that hybrids are not found in nature is not evidence that

they cannot occur. Rather, their establishment may be prevented by competition. Hybrid seeds of *Sabatia* often are smaller than normal and contain less nutritive tissue. Hybrid weakness is frequent. Even if hybrids were established, gene exchange would be restricted by F_1 sterility barriers.

PATTERNS OF DISTRIBUTION

The majority of *Sabatia* species is found in or restricted to the Coastal Plain, an area which has been available for plant occupancy since early Tertiary time (Core, 1938; Braun, 1964). Lower Tertiary communities contained a relatively high proportion of tropical or subtropical species. By the Eocene, a temperate flora was probably the dominant community in southeastern United States (Graham, 1964). Later events involved expansion of the temperate flora as the Tertiary seas receded, evolutionary development and speciation, and rearrangement of communities during the Pleistocene. It is unlikely that the effect of Pleistocene climatic changes on the southeastern flora was extensive (Graham, l.c.).

Kearney (1900), Fernald (1931), and Core (1938) have postulated that many floristic elements of the southeastern Coastal Plain are derived from an ancestral flora of the Appalachian region. The peneplained Appalachians underwent a series of uplifts during the early Cenozoic Era, with the result that bogs and savanna-like (i.e., hydric and xeric) habitats were eliminated. At the same time the Coastal Plain gradually emerged. Certain Appalachian species migrated to the newly available habitats on the Coastal Plain where the savannas, bogs, shallow pools, and sandy soils provided the environment in which they could survive (Fernald, l.c.).

At present only one species of *Sabatia*, *S. capitata*, is restricted to the southern Appalachians. In the past 100 years its distribution seems to have contracted to a range of mountains in northwestern Georgia and northeastern Alabama. Four other species, *S. angularis*, *S. brachiata*, *S. campanulata*, and *S. quadrangula*, grow in the Appalachian region and elsewhere.

The Ozarkian region has had much the same history as Appalachia. It was isolated from Appalachia during the Tertiary by waters of the Mississippi Embayment (Core, 1938). Ozarkia was proximal to prairie and Sonoran floras on the west, and has floristic affinities with the south and the Appalachian upland (Braun, 1964). *Sabatia campestris* is restricted to Ozarkia and regions to the south and west.

Thus, six species of *Sabatia* occur in one or the other of these refugia, or both *(S. angularis)*. The other species are distributed south and east of Appalachia and Ozarkia in the Piedmont and Coastal Plain.

Sabatia stellaris (including "*S. simulata*") occurs in Mexico as well as in eastern United States, the Bahamas, and Cuba. It likely had a wider distribution in the past and has now disappeared from Texas, where there are seemingly suitable habitats, leaving disjunct stands in Mexico. Dressler (1954) remarked that such Mexican-eastern U.S. disjunct species invaded Mexico in response to environmental stress during the Pleistocene. Rather than zonal displacement, glaciation may have caused regional extinction and disruption of the range (Webster, 1970).

Also, *S. kennedyana* may have had a wider distribution at one time. It is presently known from northeastern South Carolina, southeastern North Carolina, Rhode Island, eastern Massachusetts, and Nova Scotia. *Scirpus longii* Fern. has a similar distribution. Fernald (1943) suggested that this species and others with comparable distributions migrated along the once emergent continental shelf and were isolated when the shelf became submerged.

The varieties of *S. macrophylla* are separated in Georgia by no more than 50 miles, but in Florida they are absent in the area between Tallahassee and Lake City. Ward (1967) said, "The absence of an otherwise widespread species in the area between Leon and Columbia counties is a frequent feature of plant and animal distribution in Florida." Repeated atempts to locate *S. macrophylla* in this region have been unsuccessful. As Ward noted, the area was occupied by an embayment of the Gulf of Mexico during Pleistocene interglacial periods (MacNeil, 1950). At times of greatest

inundation the embayment isolated peninsular Florida and extended across southeastern Georgia (Ward, l.c.). Probably as a result the populations of *S. macrophylla* were isolated from one another and became weakly differentiated. The closely related *S. difformis* has a similar gap in Floridean distribution, but populations are not morphologically discontinuous. The fact that other species *(S. bartramii, S. campanulata, S. gentianoides)* are also absent between Leon and Columbia counties suggests microenvironmental unsuitability.

The remaining species of *Sabatia* have rather conventional Coastal Plain patterns of distribution. The species probably arose from one or more ancestral taxa which existed in the Appalachian refugium in Tertiary times or before. They possibly evolved in the Appalachian highlands and migrated to the Coastal Plain or, alternatively, evolved in the Coastal Plain from earlier migrants.

TAXONOMIC RELATIONSHIPS

As with almost all species, those of *Sabatia* were originally recognized by morphological discontinuities. The experimental data presented here leave no doubt that the species *per se* are discrete phyletic units having chromosomal and genetic differences. However, arrangement of species in the systematic hierarchy followed heretofore and recognition of varieties are subject to re-examination.

Section SABATIA

Subsect. DIFFORMES. This subsection is maintained without change. The species (*S. difformis* and *S. macrophylla*) are perennials and closely related; crossability barriers are not stringent. Fertility of hybrids is unknown. The species cross rather freely with members of two other subsections, *S. quadrangula (Angulares)* and *S. brevifolia (Campanulatae)*. It may not be coincidental that these four species are exclusively white-flowered. All other species in the genus are basically pink-flowered. Blake (1915) placed *S. difformis* and *S. macrophylla* with *S. quadrangula* (as *S. paniculata*) in his subsection *Angulares*. *Sabatia brevifolia* has never been allied with these.

If the hybrids from crosses of *S. quadrangula* and members of *Difformes* are fertile, *S. quadrangula* should be allied with subsect. *Difformes*. Gleason (1952) noted that *S. quadrangula* is "very close to *S. difformis* in describable characters . . ." However, *S. quadrangula* and *S. brevifolia* have crossing and stronger morphological affinities with other species as well. For that reason they are not at present considered to belong to subsect. *Difformes*.

The two varieties of *S. macrophylla*, var. *macrophylla* and var. *recurvans*, are maintained. They have distinct geographical ranges and there is no evidence that they intergrade in nature or occur in the same population. They may be distinguished readily by the recurvation and length of colyx lobes. These differences are retained by cultivated plants grown under uniform conditions. Specific status (*cf.* Small, 1933) is not justifiable in view of their close morphological, cytological, and crossability relationship.

Subsect. ANGULARES. Members of *Angulares* do not have strong crossing affinities, but they are morphologically related and are biennials. *Sabatia angularis* and *S. quadrangula* (characterized in part by pink and by white corolla lobes, respectively) are closely related morphologically; but they are strongly differentiated in terms of crossability and chromosome number. *Sabatia brachiata* (with pink corolla lobes) is more remote from *S. angularis* in both morphology and chromosome number. The similarity in chromosome numbers does not justify reconsideration of taxonomic rank for *S. brachiata* and *S. quadrangula*. The two are readily distinguished morphologically. The cytological races of *S. quadrangula* are not phenotypically differentiated and are not given taxonomic recognition.

Members of *Angulares* seem to have a transitional crossing relationship with the other subsections as here delimited. *Sabatia brachiata* crosses with members of *Campanulatae* and *Dodecandrae*. *Sabatia quadrangula*, in addition to crossing with *Difformes*, produces sterile hybrids in crosses with *S. stellaris (Campanulatae)*. *Sabatia angularis* crosses with *Campanulatae* members and with *S. dodecandra* var. *foliosa (Dodecandrae)*. Thus, no clear pattern emerges

which would justify allying these species with those of other subsections. Members of *Angulares* may be nearest among extant species to the ancestral stock of *Sabatia* since they bridge the gap between annuals and perennials as far as crosses are concerned.

Subsect. CAMPANULATAE. In the *Campanulatae* all species except *S. brevifolia* are intercrossable, and certain hybrids are partially fertile. Seeds are produced by crosses involving *S. brevifolia*, but they are small and the seedlings are weak. Nonetheless, crossability in certain directions is high. On these and morphological grounds *S. brevifolia* is kept in subsect. *Campanulatae*.

The other three species traditionally placed in *Campanulatae* are intercrossable and more closely related to each other than to *S. brevifolia*. Wilbur (1955) considered *S. grandiflora* (n=18) closer to *S. stellaris* (n=18) than to *S. campanulata* (n=17). This conclusion is supported by chromosome numbers and crossability relations. However, hybrids from the cross *S. grandiflora* (♀) × *S. stellaris* are sterile whereas those involving *S. stellaris* and *S. campanulata* are semi-fertile. In the latter crosses the partial sterility is probably due to imbalance resulting from differences in chromosome number of the parental species. The sterility of hybrids from *S. grandiflora* × *S. stellaris* may be more fundamental, resulting from disharmonies between the genomes differing genetically or structurally. It is apparent that crossability and hybrid fertility are not correlated positively in all instances.

Gleason (1952) remarked that *S. stellaris* ". . . and *S. campanulata* constitute the local extremes of a variable population which may represent only one species or as many as four," the others being *S. brevifolia* and *S. gracilis* (Michx.) Salisb. Wilbur (1955) reduced *S. gracilis* to synonymy with *S. campanulata*, and this decision is supported by my field and greenhouse observations. Greenhouse progeny of the "*gracilis*" type take on the typical growth form of *S. campanulata* (*see* synopsis of taxa) and chromosome numbers are similar (n=17). *Sabatia campanulata* is perennial; the other two species are annual, and

all three differ in chromosome number, crossability, and morphology. They cannot be considered a single variable population.

Britton (1905) and Britton and Millspaugh (1920) recognized two species of *Sabatia* as growing in the Bahamas, "*S. campanulata*" and the supposed endemic "*S. simulata*." The latter species was distinguished from pink-flowered "*S. campanulata*" by its smaller, white flowers and more slender habit (*see* synopsis of taxa). Wilbur (1955) referred "*S. simulata*" and the pink-flowered Bahamian populations to *S. stellaris*. Collections of *Sabatia* from islands of Abaco, Eleuthera, Grand Bahama, and New Providence were made for this study. Chromosome numbers of the color phases are the same as *S. stellaris* and no combination of characters adequately delimits all Bahamian specimens from the mainland *S. stellaris*.

Reduced crossability of the Bahamian taxon and mainland *S. stellaris* suggests that genetic changes have accumulated in the spatially isolated populations. Most of the crosses reported here involved plants from New Providence Island. Average pollen fertility of the hybrids was somewhat lower than that of the parental species (Table 3). But the values include viability estimates made early in the flowering season. Subsequent estimates were much higher and indicate that there is no substantial reduction in hybrid fertility. As Wilbur noted, formal taxonomic recognition of the Bahamian populations is not justified. All are referable to *S. stellaris*.

Plants from the Abaco "whitelands" do seem to have stronger barriers to crossing with *S. stellaris*; plants are more distinctive morphologically than are those from New Providence. The Bahamian populations of *S. stellaris* constitute geographical races which are gradually diverging genetically from the mainland populations.

Sabatia calycina is transferred from subsect. *Dodecandrae* to *Campanulatae*. Blake (1915) placed it with pentapetalous species in *Campanulatae*; the species was transferred to subsect. *Dodecandrae* by Wilbur (1955). Morphological evidence is subject to either interpretation.

Cytological evidence has not resolved the dispute over placement of *S. calycina*, but its crossing relationships are clearly with members of the *Campanulatae*. There is no evidence that it crosses readily with members of *Dodecandrae*.

Sabatia calycina is a polyploid (n=32). Its regular meiosis with no evidence of multivalents suggests it is a balanced allopolyploid. As yet there is no information with regard to its origin.

Subsect. DODECANDRAE. Members of *Dodecandrae*, with *S. calycina* excluded, show strong crossability with one another. They are polypetalous and perennial.

Ahles (1964) reduced *S. kennedyana* (n=20) and (as var. *coriacea*) *S. bartramii* (n=18) to varietal rank under *S. dodecandra* (n=17). He placed *S. harperi* Small, a synonym of *S. foliosa* Fern. (= *S. dodecandra* var. *foliosa*; n=19), in the synonymy of *S. dodecandra* var. *dodecandra*. The transfer of rank was effected by citing the basionym, and no justification was presented for the change. Though the taxa are intercrossable, they differ in chromosome number; fertility of artificial hybrids, where known, is low (pollen viability 1.6% or less). *Sabatia bartramii* and *S. dodecandra* var. *foliosa* are largely sympatric but natural hybrids do not occur. *Sabatia dodecandra s. s.* and *S. kennedyana* are distinctive ecologically and geographically. The morphological features separating these taxa are as strong as characters distinguishing members of other subsections. There is no justification for recognizing *S. kennedyana* and *S. bartramii* as varieties (*see* Wilbur, 1970, for further discussion).

Wilbur (1955) reduced *S. foliosa* (n=19) to varietal rank under *S. dodecandra* (n=17 + 2 pairs accessory chromosomes). If the cytological difference proves to be stable throughout the respective ranges and if hybrids are sterile, a reconsideration of specific rank should be undertaken (*see* Wilbur, 1970); additional work is in progress. The taxa are strongly dissimilar ecologically and occupy distinctive geographical ranges.

Section PSEUDOCHIRONIA

The two members of *Pseudochironia* were at one time segregated in a separate genus, *Lapithea* (Grisebach, 1845; Small, 1903, 1933). There are morphological differences of a higher order of magnitude between members of sect. *Pseudochironia* and subsect. *Dodecandrae* than within *Dodecandrae*. However, sect. *Pseudochironia* does not have the reproductive isolation of sect. *Campestria*, to follow. *Sabatia gentianoides* (n=14), as noted previously, crossed with members of subsect. *Dodecandrae* (sect. *Sabatia*). *Sabatia capitata* (n=38) crossed with *S. dodecandra* var. *foliosa* (n=19) and with *S. bartramii* (n=18). Sectional rank best expresses the morphological discontinuities while generic rank obscures the obvious phylogenetic relationship to subsect. *Dodecandrae*.

Sabatia capitata is believed to be a relict amphiploid. The relationship of *S. capitata* and *S. gentianoides* is unclear. *Sabatia capitata* is probably more primitive than the Coastal Plain *S. gentianoides* which has reduced and modified foliage (Wilbur, 1955). The two have widely diverse chromosome numbers and are not intercrossable. They may be related through a common ancestor from which *S. gentianoides* has evolved by a chromosomal reduction series.

Section CAMPESTRIA *stat. nov.*

Subsect. *Campestres* Blake, Rhodora **17**: 65. 1915.

Neurola Raf., New Fl. 4: 92. 1838.

The *Campestres* group is worthy of sectional rank. *Sabatia campestris* (n=13) and *S. arenicola* (n=14) seem to represent a now well differentiated line of evolution in the genus. They are genetically isolated from other members of the genus and for the most part they are geographically isolated as well. Only *S. angularis* and *S. campestris* overlap in distributions. The chromosome numbers are the lowest in the genus with the exception of *S. gentianoides* (n=14) which is not closely related either morphologically or genetically. This evidence, when combined with that of morphology, suggests a greater evolutionary hiatus between these species and members of sect. *Sabatia* than is implied when *Campestres* is placed in sect. *Sabatia*.

Considering its present distribution, the outbreeding *S. campestris* may have originated from an Ozarkian ancestor. On morphological grounds, the inbreeding *S. arenicola* is closely related, although the two are genetically isolated from each other. *Sabatia arenicola* probably originated as a self-pollinating race from an ancestral outcrossing race. In view of its present littoral habitats in Texas and Mexico, catastrophic selection for early maturing genotypes may have occurred (cf. Lewis, 1962).

Although *S. arenicola* now grows only on recent (Quaternary) land deposits, there were earlier shore lines on which it could have evolved. There is, therefore, no reason to assume a recent origin for the species. Its lack of crossability with *S. campestris* supports this assumption.

Section *Campestria* is most closely related to subsect. *Angulares*. Species in both groups have quadrate stems margined at the angles by a thin membrane, together with other characteristics in common (*see* Wilbur, 1955).

Sabatia is usually placed near *Centaurium* Hill in taxonomic treatments of the family. The relationship is closest through sect. *Campestria* whose members extend into the easternmost range of *Centaurium*. *Sabatia arenicola* bears a striking, if perhaps superficial, resemblance to certain Centauriums. This line of evolution may be interrelated with that of *Centaurium*.

DISCUSSION

The hybridization program has been most useful in testing the validity of taxonomic groupings and in elucidating patterns of relationship. In general, views of discontinuity denoted by the supraspecific divisions of Wilbur (1955) are supported by these data. There are several species (*S. brachiata*, *S. brevifolia*, *S. calycina*, *S. gentianoides*, and *S. quadrangula*) which show greater inter(sub)sectional than intra(sub)sectional crossability. Certain ones of these partially bridge morphological and cytological gaps between the subsections or sections involved. They may represent steps in evolutionary series of anastomoses in a phylogenetic web (*cf.* Levin, 1966).

The occurrence of unequal viable seed set in reciprocal crosses has been reported in recent papers by Mason (1952; *Limnanthes*), Grant (1956b; *Gilia*), Vickery (1959; *Mimulus*), Vasek (1964; *Clarkia*), Ellison (1964; *Bahia*), and Levin (1966; *Phlox*). Reciprocal differences often are correlated with differences in style length or with cytological abnormalities or sterility factors. None of these accounts for unequal reciprocal crossability in *Sabatia*. Analysis of *Sabatia* crosses shows that, in addition to unequal seed set, dissimilar hybrids may result from reciprocal crosses.

There may be in *Sabatia* a cytoplasmic or maternal influence on morphology and seed formation similar to that noted in *Gilia* (Grant, 1956b). Since most of the crosses have been heteroploid, there are ploidal influences as well. In this study 51 reciprocal heteroploid crosses had unequal seed set. Of these, 37 or 73% had a higher seed set when the pollen parent was of lesser ploidy than the pistillate parent.

The difference in chromosome number is in itself a barrier to formation of fertile hybrids in *Sabatia*. This barrier does not necessarily operate at the level of initial crossability. While heteroploid crosses do not give a true indication of genetic relationship, they show that aneuploidy has been an effective source of karyological variation leading to reproductive isolation among closely related species and, presumably, to species formation.

Basic chromosome numbers known in the Gentianaceae are x = 5, 6, 7, 8, 9, 11, 12, 13, 15, and 17 (Löve, 1953; Darlington and Wylie, 1955; Khoshoo and Tandon, 1963). Numbers of x = 5, 7, 9, and 13 seem to be, in occurrence, the principal basic numbers. Chromosome numbers are known for about 130 species belonging to 20 genera (Khoshoo and Tandon, l.c.), approximately 19% of the total species (700) in the family.

The number x = 13 has been explained in different ways. Favarger (1949) suggested that the number 13 was derived from x = 7 through polyploidy followed by fusion of two chromosomes. He assumed that the original number of the family was x = 5 and that the higher number of

x = 11 was derived through polyploidy followed by fragmentation.

Skalinska (1952; reviewed in Löve, 1953) found a basic number of x = 6. According to Löve (l.c.) and Khoshoo and Tandon (1963), the numbers 11 and 13 more likely are secondary basic numbers which have been compounded from 5 + 6 and 6 + 7 respectively. Thus, the numbers 5, 6, and 7 are primary basic numbers in the family.

In *Sabatia* the basic number could be 7. By remote and now concealed polyploidy (Darlington, 1956) tetraploids and hexaploids may have arisen. Through these the array of chromosome numbers now known for contemporary species could have been derived by aneuploid reduction and secondary polyploidy.

The wide variation in basic chromosome numbers of Gentianaceae shows that generic diversification has been based largely on alloploidy (Löve, 1953). In her opinion evolution at the species level has been based on formation of abrupt-species by polyploidy and on gradual evolution of species with identical chromosome numbers. To these may be added aneuploidy in *Sabatia* and in *Swertia* (Khoshoo and Tandon, 1963). The two polyploids in *Sabatia* support the argument of Rork (1949) that, in Gentianaceae, polyploids have neither a wider distribution nor a more northern distribution than that of diploids.

The experimental data presented here strengthen impressions of morphological discontinuity among species of *Sabatia*; reproductive discontinuities are strictly correlated with those phenotypic characteristics which differentiate species. There is no hybridization in nature although an outcrossing system prevails and vigorous hybrids can be obtained artificially with some facility. External barriers to hybridization include ethological, seasonal, spatial, and ecological isolation. While internal crossability barriers are stronger among sympatric species than among allopatric ones, sterility barriers to back-crossing or formation of advanced generation hybrids are generally stringent in either case. The occurrence of natural polyploidy and of strong crossability or sterility barriers, together with its lack of

cytological uniformity, indicate that *Sabatia* is a genus at an advanced stage of evolution and of considerable age.

ACKNOWLEDGMENTS

I thank the following persons who collected live plants or cytological material of *Sabatia*: Sylvia A. Earle, P. F.-C. Greear, Olga Lakela, R. W. Long, Barbara M. Grigg, D. E. Stone, and R. L. Wilbur. Dr. J. W. Berry identified the flower spiders.

Although this study was not based upon herbarium specimens, I have examined a number of collections. For this courtesy I wish to thank curators of the following herbaria: DUKE, FLAS, FSU, GA, NCU, NSC, TENN, US, and USF.

The guidance of Drs. Donald E. Stone and Robert L. Wilbur is gratefully appreciated.

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THE SYSTEMATICS AND ECOLOGY OF POISON-IVY AND THE POISON-OAKS (TOXICODENDRON, ANACARDIACEAE)

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(Continued from page 237)

4g. **Toxicodendron radicans** subsp. **divaricatum** (Greene) Gillis, stat. nov. Fig. 44.

Toxicodendron divaricatum Greene, Leafl. Bot. Observ. Crit. **1:** 122. 1905. *Rhus divaricata* (Greene) McNair, Publ. Field Mus. Nat. Hist. 225, Vol. 4: 69. 1925, non Eckl. and Zeyh., Enum. Pl. Afr., p. 146. 1834. *Rhus greenei* McNair *(ibid.)*, insert after page 69. *Toxicodendron radicans* var. *divaricatum* (Greene) Barkley (as *divaricata*), Ann. Missouri Bot. Gard. **24:** 433. 1937. *Rhus radicans* var. *divaricata* (Greene) Fernald, Rhodora **43:** 596. 1941. Type: *Purpus*, s.n., Mexico, Calmalli, Baja California Norte, 700-900 feet. Jan.-Mar. 1898. (US-383431, lectotype of Barkley, 1937).

Rhus tridentatum Sessé and Moçiño, Pl. Nov. Hisp., p. 47. 1887. non Thunb. ex L.f. Suppl. 184. 1781, nec Sond. ex Harv. and Sond., Fl. Cap. 1: 511. 1859, nec Willd. ex Engler in DC., Monogr. Phanerog. 4: 438. 1883. *Rhus saxatilis* DC. Prodr. 71. 1825. Type: "Habitat in calidis Nouae Hispaniae regionibus, et capite Bonae Spei. Floret uere." (MA, lectotype; F-1572884, photograph of type).

Toxicodendron laetevirens Greene, Leafl. Bot. Observ. Crit. **1:** 123. 1905. *Rhus radicans var. laetevirens* (Greene) Fernald, Rhodora 43: 596. 1941. Type: *J. W. Toumey*, s.n. Arizona, Pima Co., Santa Catalina Mts., 5 May 1894. (US-441725, holotype; A, GH, NY (3 specimens), US-619140, isotypes; MO-144536, photograph of type).

Toxicodendron phaseoloides Greene, Leafl. Bot. Observ. Crit. **1:** 123. 1905. Type: *C. V. Hartman* 102. Mexico, Sonora, Turicachi, 5600 feet altitude, 7 Dec. 1890. (US-306157, holotype; GH, NY, isotypes).

Toxicodendron arizonicum Greene, Leafl. Bot. Observ. Crit. **1:** 123. 1905. Type: *Edward Palmer* 453a, Arizona,

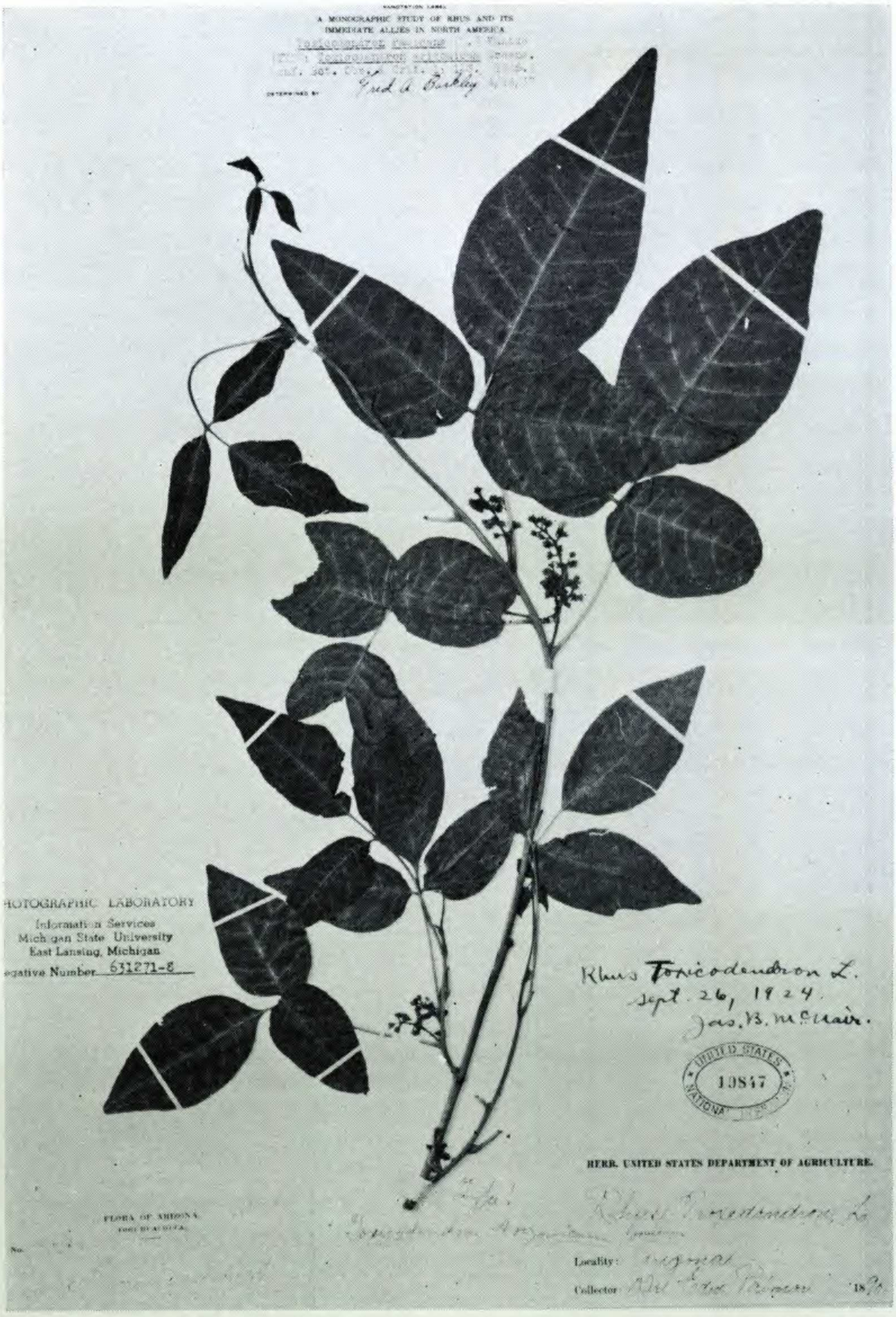

Fig. 44. *Toxicodendron radicans* ssp. *divaricatum*. Holotype of *Toxicodendron arizonicum* Greene, *Palmer*.